THESIS FOR THE DEGREE OF DOCTOR OF SCIENCE, SUBMITTED THROUGH THE DEPARTMENT OF AGRICULTURAL AND FOREST ZOOLOGY, UNIVERSITY OF EDINBURGH.

"STUDIES ON THE NATURAL CONTROL OF NOXIOUS WEEDS AND INJURIOUS INSECTS, WITH SPECIAL REFERENCE TO INSECT PARASITES."

BY

EWEN CAMERON, B.Sc., Ph.D.

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C O N T E N T S.

SUPPORTING PAPERS.

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FOREWORD.

During the past eleven years the author of the following papers has been employed by the Imperial Institute of Entomology, at Farnham House Laboratory, on the Natural and Biological Control of Plant and Insect Pests. For the greater part of this time he has been chief assistant to Dr. W.R. Thompson, F.R.S., the noted Biological Control expert, and is now, at the time of writing, Acting Superintendent of the Laboratory. This Laboratory, which is generally recognised to be the chief organisation for work on the Natural and Biological Control of noxious weeds and injurious insects in the world, is mainly occupied with the control of various introduced Dominion and Colonial pests of agriculture and forestry. The severity of these pests is attributed to the absence of their natural enemies, and it is the chief business of the staff of Farnham House to secure these beneficial insects for shipment to the affected countries. This work involves a study of the pest - weed or injurious insect - in its native habitat, and a thorough exploration of the best methods of collecting, rearing, and shipping, the most promising phytophagous and entomophagous insects (parasites and predators) for control purposes.

Since its inception, some thirteen years ago, the members of the Laboratory staff have handled more than thirty projects, involving a considerable amount of specialized entomological research. They have published about ninety papers, and have dispatched the vast total of nearly forty million beneficial insects to all parts of the globe, including Great Britain, Northern Ireland, Canada, Australia, New Zealand, South Africa, Eire, India, Kenya, West Indies, Cyprus, Fiji, Falkland Islands, Ceylon, Mauritius, Malta, the United States of America, and certain European states.

The great variety of work which has been carried out at Farnham Royal has enabled the staff to gain wide experience in this important method of pest control. During the last eleven years, the present writer has been engaged, in one way or another, on the majority of the problems submitted to the Laboratory for solution. He has been mainly responsible for the weed control work (with the exception of the preliminary period, when it was handled by Dr. A.D. Imms at Rothamsted), and entirely responsible for the investigation of the following projects : Pea Moth (Cydia nigricana Steph.); Holly Leaf-miner (Phytomyza ilicis Curt.); Beech Coccus (Cryptococcus fagi Baren.); Pine Chermes (Chermes pini L.); Balsam Bark Louse (Dreyfusia piceae Ratz.); and Swift Moths (Hepialus spp.). For two successive years he worked on Canada's most important forestry pest, the White Spruce Sawfly (Diprion polytomum Htg.).

This involved extensive travelling in continental countries such as Czechoslovakia, Germany, Austria and Hungary, with a consequent useful enlargement in personal experience of biological control work in new fields. These expeditions resulted in the discovery of many important parasites which were shipped to Canada in immense numbers. Other projects on which he has been engaged at various times are the Pine Shoot Moth (Rhyacionia buoliana Schiff.), the Larch Case Bearer (Coleophora laricella Hb.), and the Hawthorn Scale (Lecanium coryli L.), etc. Altogether, the diversity and number of projects investigated, the large geographical and ecological areas traversed and retraversed in the study of insect pests, and the mass collection of parasites and predators from Achterneed in Western Ross-Shire to Budapest in Hungary, has enabled the author to accumulate a great deal of useful experience in the methods of natural and biological control.

In addition to investigations on Dominion and Colonial pests, a certain amount of work was carried out for Great Britain on the control of native pests; e.g., a Chalcid parasite of the Spruce and Pine Sawflies, Microplectron fuscipennis Zett., which did not occur in this country, was distributed by the author to forests in Ross-Shire and Norfolk.

The papers contained in this Thesis aim at illustrating the three most important aspects of biological control.

I. The control of noxious weeds by phytophagous insects.

II. The control of injurious insects by entomophagous insects.

III. The study of insect parasites, especially in their developmental stages. (A knowledge of these immature stages is absolutely essential to the proper handling of the insects both in the country of collection and of liberations).

The term 'Natural Control' is generally understood to mean the check exerted on the multiplication of organisms by natural as opposed to artificial environmental factors. It includes all the factors (apart from artificial) both animate and inanimate, which tend to reduce the numbers of the pest in question. 'Biological Control', on the other hand, takes into account only the living or biotic factors, and these, because of the comparative ease with which they can be handled, are usually reduced to the indigenous insect enemies - parasites and predators - and, in the case of weeds, phytophagous insects. Although these insect enemies are of prime importance, the other factors operating on the pest in question, must on no account be neglected. In the following papers, therefore, the various problems have been treated, so far as possible, from the wider natural control point of view.

The general principles underlying the biological control of insect pests have been thoroughly dealt with by various writers, including Dr. W.R. Thompson, Dr. A.D. Imms, H.S. Smith, etc., etc., while a textbook on the subject was

recently published by H.L. Sweetman, so that it would be mere vain repetition to go over this ground again. In the Ragwort paper, however, the principles of weed control by phytophagous insects have been laid down, and the general methods of dealing with an insect pest are embodied in the publication on the Pea Moth.

As already pointed out, the recognition of the immature stages of the various parasites is all important in work of this kind, and a great deal of time has been devoted to the study of these. Examples of this work may be found in the following papers, but especially in No. 3, where some curious formations are described.

With regard to the two supporting papers, it may be stated that the present writer was responsible for all the work done on Microplectron fuscipennis (No.4), with the exception of the account of its distribution, and part of section eleven. His share in paper No. 5 consisted of the data relating to the following parasites : Microcryptus basizonius, Hemiteles areator, Delomerista sp., Pimpla alternans, Lamachus sp., and part of the descriptions of most of the others. He was also mainly responsible for the formation of the keys to the various parasites.

The present position of the various beneficial insects described in the following papers may be briefly summarized as follows. Tyria jacobaeae does not appear to be exerting any

appreciable effect on Ragwort in New Zealand, chiefly because of the attacks of native parasites. The Anthomyiid seed-fly, Pegohylemyia seneciella is still being experimented with, and according to the New Zealand authorities, is showing hopeful signs of usefulness. Before control of this weed can be obtained, however, the various measures advocated in the following paper, such as the elimination, so far as possible, of factors predisposing to open soil conditions, etc., must be carried out. News has just been received that the Pea Moth parasites sent from this country to Canada, have become established and great hopes are entertained for the successful outcome of this experiment in biological control. Opius ilicis, Microplectron fuscipennis, Microcryptus basizonius, and many other parasites have become established in Canada as a result of our introductions, and many of them are already exerting some measure of control. It may be interesting to note that the Chalcid, Microplectron fuscipennis, is now being bred on factory proportions in special insectaries at Belleville, Ontario, and millions of these useful parasites are being produced there for distribution to various parts of Canada.

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I.

A STUDY OF THE NATURAL CONTROL OF RAGWORT (*SENECIO JACOBAEA* L.)

BY

EWEN CAMERON, B.Sc., F.R.E.S.

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A STUDY OF THE NATURAL CONTROL OF RAGWORT (*SENECIO JACOBAEA* L.)

BY EWEN CAMERON, B.Sc., F.R.E.S.
(*Imperial Institute of Entomology.*)

(*With Plates XX, XXI and eleven Figures in the Text.*)

CONTENTS.

INTRODUCTION.

WITHIN the last ten or twelve years that branch of economic entomology which aims at the suppression of noxious weeds by the application of biological measures has come to occupy an increasingly prominent position in the field of Empire research. More especially is this true of the countries "down under"—New Zealand, Australia, and the islands of Fiji—where extensive studies and field operations on the problem of controlling various introduced weeds by the agency of phytophagous insects have been carried out.

Weeds may be defined economically as plants which are not only useless to man, but are also injurious to crops and stock reared by man. Wherever agriculture exists, weeds occur. They vary greatly in importance, but even when they are relatively innocuous in their native homes, they often become extremely injurious when introduced into new environments. In these new environments, freed from the restricting influences which held them in check in the homeland, they rapidly assume the proportions of pests, provided of course that restrictive influences equal in potency to those of the homeland are not present. It is to the weed pest, characteristic of these conditions, that biologists are attempting to apply the method of natural control.

The present paper comprises a short account of the New Zealand Weed Control Scheme, a summary of previous attempts to subjugate weeds by the biological method, a study of the ecology and natural control of ragwort (*Senecio jacobaea* L.), a weed accidentally introduced from Europe into several other parts of the world, a description of the methods used in dealing with the natural enemies of this plant, and a discussion of the possibilities of biological control in the particular species under consideration.

I. THE BIOLOGICAL CONTROL OF WEEDS IN NEW ZEALAND.

The attempt to control weeds in New Zealand by the biological method was initiated by Dr R. J. Tillyard, who, in 1927, with the help of grants from the Empire Marketing Board, the New Zealand Government, and the Cawthron Institute Trustees, established a laboratory for this purpose at the Cawthron Institute, Nelson, New Zealand. In Europe, the initial investigations were mainly carried out at the Rothamsted Experiment Station by entomologists working under the supervision of Dr A. D. Imms; later, in 1929, this work was transferred to the Parasite Laboratory of the Imperial Institute of Entomology at Farnham Royal, where Dr A. S. Watt and Mr E. H. Chater carried out an investigation on gorse, and the present writer on ragwort.

The noxious plants brought under this Weed Control Scheme consisted of the four major weeds: *Senecio jacobaea* L. (ragwort), *Ulex europaeus* L. (gorse), *Rubus fruticosus* (agg.) L. (blackberry), and *Acaena sanguisorbae* (piri-piri or bidi-bidi). Later *Pteridium aquilinum* L. (Kuhn) (bracken), *Digitalis purpurea* L.

(foxglove), *Hypericum perforatum* L. (St John's wort), *Rumex* spp. (dock), and *Urtica dioica* L. (nettle) were included. All these weeds, with the exception of piri-piri, are native to Britain. Work has been carried out at Farnham Royal on ragwort, gorse, blackberry, and, to a lesser degree, on bracken. The present position of the work is summarised as follows:

Ragwort. The control of this weed being the subject of the present investigation, all details come later.

Gorse. Since gorse is useful for sheep fodder and also for supplying nitrogen to the soil, only partial control is desired. For this purpose the weevil, *Apion ulicis* Först., is being used. The larvae of *Apion* develop in the gorse pods and destroy a considerable number of the seeds. Initial difficulties were experienced in the breeding of the weevils in New Zealand, but they have now been overcome and *Apion* has been established in the field, where it plays a definite part in the control of gorse. Other insects, such as the moth *Laspeyresia ulicetana* Haw., might prove useful means of control, but they have not yet been investigated. A report on this part of the work has been published by Mr E. H. Chater (1931).

Blackberry. This weed is a very difficult one to deal with because it belongs to the family Rosaceae, which includes a very large number of most important economic plants. Several insects studied, such as the moths, *Thyatira batis* and *Bembecia marginata*, the gall-forming Buprestid, *Agrilus ruficollis*, and the midges *Perrisia plicatrix* and *Lasioptera rubi*, were discarded because of their propensity for attacking important allied food plants. The Buprestid beetle, *Coraebus rubi* L., appeared to be the most effective of the natural enemies. The larvae of this species, which is widely distributed throughout Western, Central, and Southern Europe, though absent from the British Isles, feed on the roots of blackberry; but they also attack tea roses (*Rosa indica*) and raspberry. However, so obnoxious had the blackberry pest become, that the authorities decided to overlook the danger to roses and raspberries, and imported large numbers of the larvae of the beetle in rose stocks from the Antibes area in Southern France, via Farnham Royal. Further tests showed that the adult fed on raspberry, loganberry, rose and apple. It has not yet been liberated in New Zealand.

Other insects that might prove useful as a control occur in America, but it is now probable that the attempt to control blackberry by insects will be abandoned, owing to the great risks to economic plants from the introduced insects.

Piri-piri. The sawfly, *Antholcus varinervis*, whose larvae feed on the leaves in winter and spring, has been imported from Chile, but has not yet been liberated in New Zealand.

Bracken. The insect enemies of bracken have not yet received adequate study. The caterpillars of *Hepialus hectus* L. feed on the roots, and several species of Anthomyiidae occur on the plant; but the damage caused seems, in

general, to be insignificant, and the possibility of control by natural enemies remote.

St John's wort. The insect enemies of this weed are being investigated by the Australian entomologists. They can easily be introduced into New Zealand if they prove effective in Australia.

No work has been done on dock, nettle, or foxglove.

Thus far only preliminary work has been carried out on the New Zealand projects, and it is too early to give any definite opinion as to the final results of the researches.

II. SUMMARY OF WEED CONTROL THROUGHOUT THE WORLD.

The following table shows the extent of the chief work carried out, or being carried out, on the biological control of weeds throughout the world:

Country	Weed	Homeland of weed	Results	Chief insects concerned
Hawaii	*Lantana camara*	Mexico	Complete control in certain areas	*Agromyza lantanae* Frogg., *Crocidosema lantanae* Busck., *Thecla bazochii* God., *T. echion* L.
Australia	*Opuntia inermis* *O. stricta* *O. monacantha* *O. tomentosa* *O. aurantiaca* *O. streptacantha* (Prickly pear)	America	Prospects of control very promising	*Cactoblastis cactorum* plus bacillary rot; *Dactylopius indicus* and three strains of *D. tomentosus* (cochineals); *Chelinidea tabulata* (bug); *Moneilema ulkei* (longicorn); *Tetranychus opuntiae* (red spider)
	Hypericum perforatum (St John's wort)	Europe	Preliminary	*Chrysomela varians*, *C. hyperici*, *C. brunsvicensis*, *Lathronympha hypericana*
	Xanthium spinosum *X. pungens* (Cockle burrs)	America	Preliminary	—
	Weeds awaiting investigation: *Lepidium Draba*, *Kentrophylum lanatum*, *Inula graveolens*, *Centaurea calcitrapa*, *Echium plantagineum*, *Chondrilla juncea*. For ragwort and gorse see New Zealand			
New Zealand	*Rubus fruticosus* L. (Blackberry)	Europe	Attempt abandoned	*Coraebus rubi* L. (Buprestid)
	Senecio jacobaea L. (Ragwort)	Europe	Prospects of control promising	*Tyria jacobaeae* L., *Pegohylemyia seneciella* Meade
	Ulex europaeus (Gorse)	Europe	Prospects of control fairly promising	*Apion ulicis* Först.
	Acaena sanguisorbae (Piri-piri)	Chile	Prospects of control fairly promising	*Antholcus varinervis*
	Pteridium aquilinum (Bracken)	Europe	Preliminary investigations. Possibility of control remote	*Hepialus hectus* L. and spp. of Anthomyiidae
	Weeds awaiting investigation: *Digitalis purpurea*, *Rumex* spp., *Urtica dioica*. For *Hypericum perforatum* see Australia			
Fiji	Lantana	America	Control hopeful	*Teleonemia lantanae*
	Clidemia hirta	—	Control in certain areas	*Liothrips urichi*

III. PRINCIPLES OF WEED CONTROL BY INSECTS.

The amount of work which is being carried on by entomologists all over the world in an attempt to check the ravages of introduced insects is sufficient evidence of the widespread destruction caused to valuable crops by such pests. Since phytophagous insects cause so much harm to economic plants if accidentally introduced, it seems that the planned introduction of suitable insects may cause similar damage to non-economic or noxious plants. This is the hypothesis underlying attempts to obtain the biological control of weeds[1].

If we do not expect too much of the method, all will be well; but if, on the other hand, we hope to see a rapid and complete clearance of the weed following on insect introduction and liberation, we shall probably be disappointed. To prove this statement, let us look at the position of accidentally introduced insect pests. There are instances, such as that of the citrus industry of California, where almost complete destruction of the crops has been threatened by introduced insect pests. Such complete destruction or extinction, however, is a term employed by the cultivators with reference to the financial aspect of the problem. It does not mean that the numbers of the plant have been reduced to zero. Biologically there may be, and usually are, enough numbers left to carry on the crop, although owing to the control exercised by the insect pest, it is not able to increase and produce fruit to such an extent that its cultivation is profitable. Similarly, introduced insects are not likely to exterminate weeds. It is much harder to kill plants with phytophagous insects than it is to kill phytophagous insects with their entomophagous enemies. Furthermore, as will be shown later, plants, under certain conditions, react to insect attack. The control of plants by insects is therefore more difficult to obtain than control of insects by insects.

However, a study of the damage caused by insect pests and of the results obtained by experiments strongly suggest that the biological control of weeds, which so far has only been attempted where infested areas are so extensive that they cannot be treated by other methods, may, in certain circumstances, be possible, that under favourable conditions the increase and spread of the weed may be checked, and the infestation reduced to a level at which the infested land becomes of some economic value, even though complete destruction of the weed is not attained.

One of the first points which presents itself in an investigation of this kind is the possibility that the weed-controlling insect will migrate from its normal host, the weed, to a plant of economic value. How the insect is going to act in its new home it is impossible to say, because the new environment may affect both the insect and the plant: their relations may remain the same, may

[1] The two instances are not quite parallel because many economic plants are maintained in a man-made environment and survive only so long as man's control; many too have their constitution undermined by cultivation and breeding.

converge or diverge—one cannot tell. Certain safeguards, however, may be taken against the fulfilment of this possibility of change of host. These are: (1) the choice of an insect with a limited host range; (2) of an insect with a specialised mode of life, such as a root-borer, seed feeder, etc., when the weed is closely allied to economic plants (see Imms, 1928); and (3) the carrying out of exhaustive tests of the insects on economic plants, especially on those allied to the weed.

Host change has already occurred in agricultural practice. The Colorado beetle, *Leptinotarsa decemlineata* Say, is a good example. This insect, which originally fed on the sand burr, *Solanum rostratum*, on the eastern slopes of the Rocky Mountains, migrated to *Solanum tuberosum*, the cultivated potato, of which it became a serious and widespread pest. The beetle, before the progress of agriculture altered its environment, was confined to its native food plant, but when large areas of potatoes were planted in its vicinity it migrated to the easier and more abundant source of food supply.

The Nymphalid, *Pyrameis cardui* L., which feeds generally on *Carduus* and *Urtica*, is another instance. In Poland the transference of this species to *Lupinus angustifolium*, and in the U.S.A. to peppermint and soy beans, has been recorded.

Several experiments have been conducted to determine the possibility of such changes of host plants. Pictet (quoted by Imms, 1928) placed larvae of *Lasiocampa quercus* L., which feed on deciduous trees and bushes, on *Pinus*, and many died. The survivors bit into the extremities of the pine needles and carried through to the next generation. The larvae of this second generation became so adapted to the new host that when offered leaves of deciduous trees they either starved, or attacked them at the apices, hollowing them out in a way similar to that in which their predecessors attacked the needles of *Pinus*.

Experiments of this kind have also been made by Heslop Harrison and others. Harrison was able to effect transference of the gall-forming sawfly, *Pontania salicis*, from *Salix phylicifolia* to *S. andersonii* and *S. rubra*. Although a great deal of work has not been done on this subject, these experiments, carried out on insects with a limited host range, but general feeders on foliage and flowers and not specialised as root-borers, stem-borers, and internal seed-feeders, indicate the possibility of insects changing on to new hosts, when their environment is altered. On the other hand, several investigators, including workers on weed control, with their extensive system of starvation tests, have failed to induce phytophagous insects to adopt new hosts and transmit their acquired preference.

Generally speaking, we find that when most insects, hitherto more or less restricted in host range, attack a new host, the new food plant is closely allied to the old one, and belongs to the same family, if not to the same genus. Overcrowding of the insects and the destruction of the natural wild host are two of the causes which induce migrations to new hosts. Once established on

its new food plant, the continuity and abundance of the latter explain the ultimate outbreak of the pest.

Another point we must not forget is that by the rigid exclusion of their parasites from the new country, weed-controlling insects are given a great advantage, though sometimes this is partly offset by the attack of native parasites.

The main principles underlying the biological control of weeds may thus be summarised as follows:

(i) Since accidentally introduced insects often have an extremely destructive effect on plants of economic value, purposely introduced suitable species may exercise a similarly destructive effect on plants of no value—or weeds.

(ii) The insects selected for control purposes should preferably be effective against the weed in its home country, although it may happen that an insect which is comparatively harmless in one environment may be more virulent in another, and *vice versa*.

(iii) They must also be more or less specific, or have a restricted host range. If the weed in question is isolated systematically and physiologically from plants of economic value, the problem is greatly simplified; if closely allied, then more specialised insects (see Imms, 1928), such as root-borers, seed-feeders, etc., and not leaf-feeders, should be employed, because leaf-feeders seem, on the whole, to be less specific in their habits than root-borers, etc.

(iv) The possibility of a change of host plant must be eliminated by exhaustive tests of the insects on economic plants, especially on those allied to the weed.

(v) Parasites must, so far as possible, be eliminated before export. If the material has been exposed to the attack of parasites in the field before collection great care must be taken in the country receiving the insects to see that all parasites that make their appearance are destroyed.

The procedure involved in the study of the insect fauna of a noxious weed, with a view to its biological control, is as follows:

(i) The compilation of a list of all insects recorded from the plant.

(ii) Life-history studies of those most suitable as controlling agents.

(iii) Starvation tests of the selected insects on economic plants related to the weed to be controlled, and on other plants open to the risk of attack.

(iv) The discovery of suitable methods for large scale collecting, sorting, and shipping parasite-free material.

This procedure has been followed in the present investigation.

IV. RAGWORT (*SENECIO JACOBAEA* L.).

(1) Description of the Weed.

Ragwort (*Senecio jacobaea* L.) is a member of the large Dicotyledonous family Compositae. A native weed of Britain and an introduced species in New Zealand, it is considered injurious in both countries. Although classed as a noxious weed, the suppression of which is compulsory under the Corn Production (Repeal) Acts, 1921, it is not of major importance in this country, except in a few areas, and is more or less controlled, partly by natural, and partly by artificial means.

In Britain *Senecio jacobaea* is a common weed in all sorts of places, but chiefly on waste land and pastoral land of poor quality, on derelict agricultural land, roadsides, sand-dunes, and in certain areas on good farm pastures and meadows. On well-cultivated land it is absent; good cultivation and farming prevent its establishment. On the other hand, in New Zealand, ragwort has increased and spread so rapidly that it is now a very serious pest. It is kept under control in well-cultivated regions, but in New Zealand there are large areas of bush grasslands only partially cleared of logs and stumps, which, on account of the heavy cost, are not at present tilled; it is in these areas and in the dairy pastures, more especially, that ragwort is a nuisance, not only as an occupant of otherwise useful land, but as a poisonous plant responsible for heavy mortality in stock. "The ragwort menace", says a North Island newspaper, "has recently been causing concern among settlers of the Bay of Plenty, and in particular, the Te Puke, Whakatane, and Tauranga districts. So bad has ragwort become this autumn, that farmers have been losing large numbers of stock. The weed has taken possession of grazing land at Ngawaro and on No. 3 Road area, and has grown as tall as five and six feet. Already one farmer in the district has lost 47 head of stock since January. On one occasion, when returning with his cows for the evening milking, one farmer at Ngawaro missed seven heifers and upon investigation he found them dead. Five draught horses were also dead. Other farmers in the district have also had losses of stock."

The plant is described in Bentham and Hooker's *British Flora* as follows: "*S. Jacobaea*, Linn.—Rootstock short and thick without creeping roots. Stems two to four feet high, erect, scarcely branched except at the top. Leaves with ovate, obovate, or narrow segments, coarsely toothed or pinnatifid, the terminal ones large and confluent, the lower ones smaller and distinct, all glabrous or with a loose woolly down, especially on the under side. Flower heads rather large, of a bright yellow, in a handsome, compact, terminal corymb. Involucral bracts tipped with black, the outer ones few and very small. Florets of the ray from 12 to 15, linear-oblong and spreading, occasionally, but rarely, deficient. Achenes of the disc covered with short hairs, those of the ray glabrous."

(2) LIFE HISTORY.

The seed. The "seeds" of ragwort are, in reality, fruits, each hard fruit containing a single seed. Such a reproductive unit is called an achene. The achenes of *S. jacobaea*, which are slightly tapered at each end, more especially towards the proximal end, are 2 mm. in length, and at the middle are 0·6 mm. in breadth. The fruit coat is ridged with approximately eight ridges round the circumference. (No transverse ribs are present; those in the figure merely being a shading effect.) On each ridge is a number of small hairs, which are about 0·66 mm. long. Attached to the distal end of the seed is an ingenious wind-dispersal mechanism—the pappus. This device somewhat resembles a parachute in its action. It consists of about sixty fine hairs attached to the distal end of the pericarp, each hair being about 6 mm. in length, approximately three times as long as the seed. These filaments are provided with a fairly regular arrangement of minute spines, which point away from the seed, and are slightly longer than the breadth of the filaments to which they are attached. The basal part of each filament, for a short distance, is closely waved. This is probably connected with the release action which effects the removal of the seed from the capitulum. The working of the "parachute" depends on the relative humidity of the air, and on the velocity of the wind. With a high relative humidity the hairs come together and render the mechanism inoperative. As the amount of moisture in the atmosphere becomes less, the filaments separate and bend over to form a parachute arrangement round the seed. By means of certain mathematical calculations (Small, 1919), the most effective angle at which the hairs are bent, together with the minimum amount of wind necessary for dispersal, can be determined. Given the conditions of a low relative humidity, a wind above a certain minimum velocity, and comparative freedom from obstacles, there is no limit to the distance of dispersal of a pappose fruit. The pappus is either a modified calyx structure, or, more probably, a specially evolved mechanism.

In England the seeds ripen about the latter part of August, the time varying with the locality and with the season.

Germination. Tests made in the laboratory with seeds from Farnham Royal and Achterneed, Ross-shire, Northern Scotland, showed that 80 per cent. were viable. On damp filter paper kept at a temperature of 15° C., the seeds began to germinate on the fourth day. By the eighth day, the majority had germinated, and while one or two belated germinations occurred up to the twentieth day, after that germination ceased. In the field, germination may occur at two possible periods: at the end of August, the most usual time, or at the beginning of the growing season in spring, the seed lying dormant throughout the winter. In the first case the seedling attains a certain size, but ceases to develop during the colder months, resuming its activities in the spring.

Experiments to ascertain the relation of germination to the depth of the seed in the soil, show that the best results are obtained when the seeds are

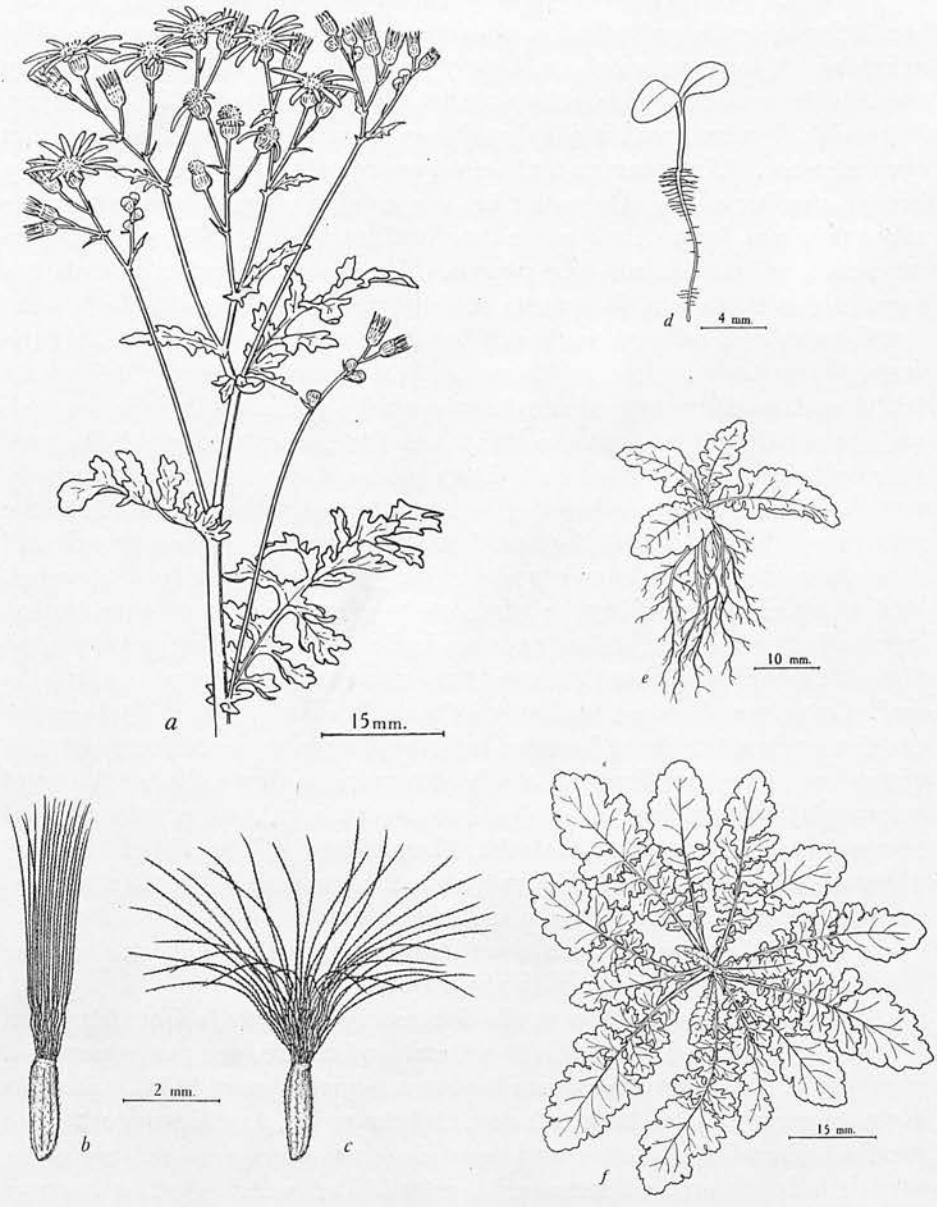


FIG. 1. Ragwort. *a*, cluster of capitula; *b*, seed with pappus closed; *c*, seed with pappus open; *d*, first stage seedling; *e*, second stage seedling; *f*, rosette.

just covered with soil. When they are buried at a depth of 1 cm. or more, no germination takes place.

The development of the seedling follows the usual course. At first two cotyledons appear, followed later by the plumule and leaves. The smooth margins of the latter soon take on the indented outline characteristic of mature ragwort. Growth continues until at the end of the first year the plant has assumed the form of a more or less flattened rosette. Just before the growing season in spring, the rosette measures 5–6 in. in diameter.

In the late spring the rosette (the plant is now in its second year) grows up rapidly to an average height of 2–4 ft., and often to 4 and 5, and sometimes even 6 ft., with one, two or more stems, which usually do not branch until near the top, where the numerous flower-heads form a compact terminal corymb. The flowers begin to open about mid-June and continue, from late secondary growth, till well on in the year, secondary flowers occurring even up to November. Pollination is effected by insect visitors, among which are the Hymenoptera *Apis mellifica*, *Bombus lapidarius*, *B. terrestris*, *B. hortorum*, *Sicus ferrugineus*, *Halictus* sp., and the Diptera *Eristalis tenax*, *Lucilia caesar*, *L. sericata*, *Calliphora erythrocephala*.

In *Senecio jacobaea*, as in other Compositae, we find an admirable adaptation for pollination. The crowding of the florets into capitula ensures that a single insect will pollinate a large number of flowers, and the earlier ripening of the male organs favours cross-pollination.

The seeds begin to set and ripen about mid-August, and are then distributed by wind. In order to ascertain the average number of seeds produced by ragwort, plants from different areas were collected and the seeds counted. It was found that the average number of seeds per capitulum was about seventy, produced from thirteen outer or ray florets, and fifty-seven inner or disc florets. Although the number of seeds per capitulum remained fairly constant from area to area, the number of capitula per plant varied tremendously, according to the size of the plant and the quality of the soil on which it grew. The figures from several areas follow:

Area	No. of capitula	Average no. of seeds	Total no. of seeds
1. Henley-on-Thames, Oxon	68	70	4,760
2. Dorney, Bucks	70	70	4,900
3. Farnham Royal, Bucks	167	70	11,690
4. Medmenham B, Bucks	191	70	13,370
5. Wentworth A, Surrey	680	70	47,600
6. Wentworth B, Surrey	910	70	63,700
7. Wentworth C, Surrey	1682	70	117,740
8. Wentworth D, Surrey	1720	70	120,400
9. Medmenham A, Bucks	2489	70	174,230

Interpreting these figures we should expect to find: plants with 5000 seeds growing either in very poor soil, or in slightly better soil where the plants are closely massed together; plants with 10,000—15,000 seeds, which is the commonest number, growing in medium to poor quality soil where the numbers of ragwort are not very high; and plants of 40,000 seeds and over growing in good soil, such as good agricultural land left derelict for building purposes, etc.

Plants producing 150,000–200,000 seeds do not often occur. The Medmenham A area figure was obtained from plants pruned the previous year, which made them three-year-old plants developing secondarily, with an unusually large production of capitula.

Ragwort is commonly known as a biennial, but I find that the length of its life period varies considerably. Generally speaking, a strong, well-grown plant, which has produced abundant seeds and is not disturbed, completes its life cycle in two years and is thus a biennial. On the other hand, a plant which has been interfered with in certain ways may become a perennial, the length of the life cycle then depending upon the action of the environmental factors affecting development. The causes most commonly producing this effect are the cutting down of the plant during agricultural operations or as a control measure, and the destruction of the flowers, leaves, and parts of the stems by phytophagous insects. Plants injured in this way, but still possessing a certain amount of reserve food, reproduce themselves by means of late secondary shoots and flowers. This secondary flower growth may result in the production of new seeds, equal to as much as 35 per cent. of the number that would have been produced by the uninjured plant, though the seed production of such plants is usually less. Where secondary flower production is not so extensive a number of basal shoots appear in the late autumn and in the spring of the following year. These shoots carry on the plant for another year, the new plants often being much larger and having more stems than the old. If this new plant of secondary origin is again cut down by man, or grazed by animals, a similar reaction takes place, and so on, till the weed finally loses all its vitality and dies. We thus have, in addition to the ordinary biennial ragwort, a very large number of individuals becoming what may be called *induced perennials.*

The spread and success of ragwort is thus principally due to: (1) the wind-dispersal mechanism—the pappus; (2) the effective multiple pollination method; and (3) the production of plants and flowers secondarily.

(3) History of ragwort in New Zealand.

Ragwort was introduced into New Zealand prior to 1874, in which year Thomson records it from Dunedin. Its increase was rapid, and it is now found in almost every provincial district in the Dominion. It had become so troublesome that it was declared a noxious weed in the first schedule of the Act of 1908.

Other introduced species of *Senecio* exist in New Zealand: *S. vulgaris* L., *S. sylvaticus* L., *S. erucifolius* L., *S. aquaticus* Huds. and *S. mikanioides* Otto.; but none of these is of great economic importance.

(4) Economic status and importance.

Senecio is the largest of the Compositae genera, being spread all over the globe, although the majority of the species occupy only small areas. Among flowering plants the Compositae, with about 900 genera and over 13,000

species, are one of the largest families, forming about one-tenth of the whole number of Angiosperms.

(i) *Economic allies.* Curiously enough, although important weeds are common among the family Compositae, food plants of economic importance are not. Those which have some economic value are merely a few minor vegetables, several plants of ornamental value, and some with medicinal properties. The food plants include lettuce (*Lactuca*), artichoke (*Cynara*), Jerusalem artichoke (*Helianthus*), chicory (*Cichorium*), etc. Amongst the ornamental plants are golden rod (*Solidago*), Michaelmas daisy (*Aster*), everlasting (*Helichrysum*), sunflower (*Helianthus*), *Dahlia*, *Chrysanthemum*, *Tanacetum*, *Cineraria*, *Calendula*, *Centaurea*, and *Echinops*. Those of medicinal value are chamomile (*Anthemis*), wormwood (*Artemisia*), coltsfoot (*Tussilago*), and *Arnica*. Within recent years *Chrysanthemum cinerariaefolium* Trev. has risen to prominence. From its dried flowers the insecticide pyrethrum is manufactured. Two other species, *C. coccineum* Willd. and *C. marschali* Ascher, also possess insecticidal properties, but *cinerariaefolium* is by far the most important. It is a native of the Mediterranean and is cultivated in Japan, which supplies 70 per cent. of the world's requirements of pyrethrum. It is also grown in France, Switzerland, and North Africa for home consumption. An attempt is being made to produce it commercially in England.

(ii) *Noxious properties.* Ragwort is injurious to farming interests in two ways. Firstly, it has taken possession of large areas of land, suitable for grazing, and, secondarily, it is poisonous to stock. *Winton Disease*, so-called from the area in Southland where it first made its appearance, is the result of eating ragwort in quantity and causes a heavy mortality in horses, and also affects cattle and sheep. A similar disease, attributable to the same species of *Senecio*, occurs amongst cattle in Pictou, Nova Scotia, where it is known as *Pictou Disease*. In Norway, *Sirasyke* is probably the same disease. All three are characterised by the same symptoms described later in this paper.

In Britain this disease is supposed to be comparatively rare. Quite recently (November 1929) in Ireland, a number of veterinary specialists presented their report to the Veterinary Medical Association of Ireland on liver cirrhosis in horses and ragwort poisoning in cattle, both affections following on the ingestion of *Senecio jacobaea* L. It appears from their researches that this type of poisoning is more common than is generally supposed. The cases noted were confined to the poorer types of pasture, where weeds, including ragwort in abundance, were present. In England several deaths have occurred among cattle as a result of eating large quantities of ragwort in dried hay. Generally speaking, however, stock, with the exception of sheep, do not eat the plant unless compelled to do so; for example, when pasture has dried up and ragwort still remains green and juicy. It is chiefly in such situations that deaths from ragwort poisoning are common in New Zealand and South Africa. In the latter country, however, two allied species, *S. retrorsus* and *S. burchelli*, are

to blame for the disease, known as *Molteno Disease*. Sheep must be placed in a separate category in regard to this malady. They are tolerant to the weed, and even eat it with avidity, so much so indeed that they have been used as a means of getting rid of the pest, often with a great measure of success. The cumulative action of the poison, however, after a long period of grazing on ragwort-infested pastures, is fatal.

(iii) *Symptoms of ragwort poisoning.* These appear after one to three months' continued grazing on the plant, and even if, at the end of this period, cattle are removed from the infested pasture, while still apparently healthy, symptoms may subsequently develop, leading to fatal results. In the early stages the animals appear hidebound, later they have a staggering gait and become partially blind. They may get very excitable and charge anyone who approaches them. In some, diarrhoea may be present, but normally constipation is very marked. At death, in the earlier stages of the poisoning, the principal lesion is an inflammation of the bowel. In acute cases the liver is firmer than normal, and yellow in colour. In chronic cases the liver is hard, owing to increase in fibrous tissue, a condition described as hepatic cirrhosis, and in those so affected the abdominal cavity contains fluid. The lungs are congested.

V. THE ECOLOGY AND NATURAL CONTROL OF RAGWORT.

Any weed-control investigation which does not take into account the influence of environmental factors (other than insects) on the weed, is far from complete. In this section an attempt is made to identify and evaluate the importance of the ecological factors determining the distribution, vigour and numbers of ragwort.

Ragwort is distributed throughout Great Britain, chiefly on light sandy soils, waste places, roadsides, sand-dune areas, derelict agricultural land and overgrazed pastures. To the ecologist this distribution indicates ragwort to be a plant which requires for its establishment a disturbed soil surface, where the plant community has been broken. Of the four groups of ecological factors affecting plants (climatic, physiographic, edaphic and biotic), the biotic is by far the most important in setting limits to the distribution of ragwort. The edaphic and climatic are important in so far as they affect the vigour of the weed and of its competitors, while the physiographic, for the purpose of this investigation, is relatively unimportant.

(1) Climatic controlling factors.

In Britain, ragwort is fairly abundant in favourable habitats, from the south coast of England up to Sutherlandshire in Scotland, and probably to the northern seaboard. It grows in areas of low and of high rainfall. Plenty of sunlight is necessary, as ragwort is normally a plant of open situations, and the seedling dies if deprived of the necessary light intensity by taller growing plants.

It must not be forgotten that the four groups of ecological factors interact. Rainfall influences and alters the edaphic factor, which in its turn reacts on the biotic, while the latter is also directly affected by climate. Bearing all this in mind, we can say that the climate of Britain is well within the range necessary to ragwort, although variation in the weather affects its vigour and recuperative powers.

(2) EDAPHIC CONTROLLING FACTORS.

Ragwort is essentially a plant of well-drained and even dry soils. It grows on the shallow, highly calcareous soils derived from chalk (*vide* Watt), on sand-dunes, on chalky sands, on derelict arable land, and neglected and overgrazed enclosed pastures. Some of these soils contain much calcium carbonate and are alkaline, and we may assume the rest to contain some free calcium carbonate and to have a low acidity. Ragwort, on the other hand, is absent from the very acid carbonate-free sandy soils of parts of Breckland. It would thus appear that ragwort grows more commonly on soils of low acidity. Yet it is found on certain somewhat anomalous soils of the Chiltern plateau, where the soil is a loam, is fertile, highly acid (*p*H 5·2–4·7), contains no free calcium carbonate, and has a low exchangeable calcium content, and a low basicity. The one factor common to all the habitats is a well-drained soil.

Within the soil range of ragwort, its frequency bears no relation to soil type, but is closely correlated with the area of bare soil offered for seed germination and seedling establishment. In naturally open plant communities, like the earlier stages of vegetation on sand-dunes, ragwort is frequent; its high frequency in other normally closed plant communities is due to the breaking of the vegetation cover by the direct and indirect interference of man; in short to the biotic factor.

(3) BIOTIC CONTROLLING FACTORS.

The influence of biotic factors on ragwort control and distribution is of considerable importance. Two groups of such factors, one botanical and the other zoological, may be recognised.

(α) **Botanical.**

Field observations. Most of the plants which have an important influence on ragwort belong to the family Gramineae. In Britain ragwort is absent from well-managed pastures on fairly good soil; long grass or close continuous turf effectively prevent its establishment, even although seed may be abundant. This was clearly demonstrated in the summer of 1930 at Hambledon, Bucks., and Buckenham, Norfolk. At Hambledon a field was divided into three natural areas of approximately ten acres each. Area 1 had a long thick sward of the grass, *Brachypodium pinnatum* L. (false brome), and was devoid of ragwort. Area 2 was a much overgrazed pasture, consisting of the following grasses:

Holcus mollis, *H. lanatus*, *Anthoxanthum odoratum*, *Dactylis glomerata*, *Phleum pratense*, *Lolium perenne*, and *Poa trivialis*. This area bore 4000 ragwort plants

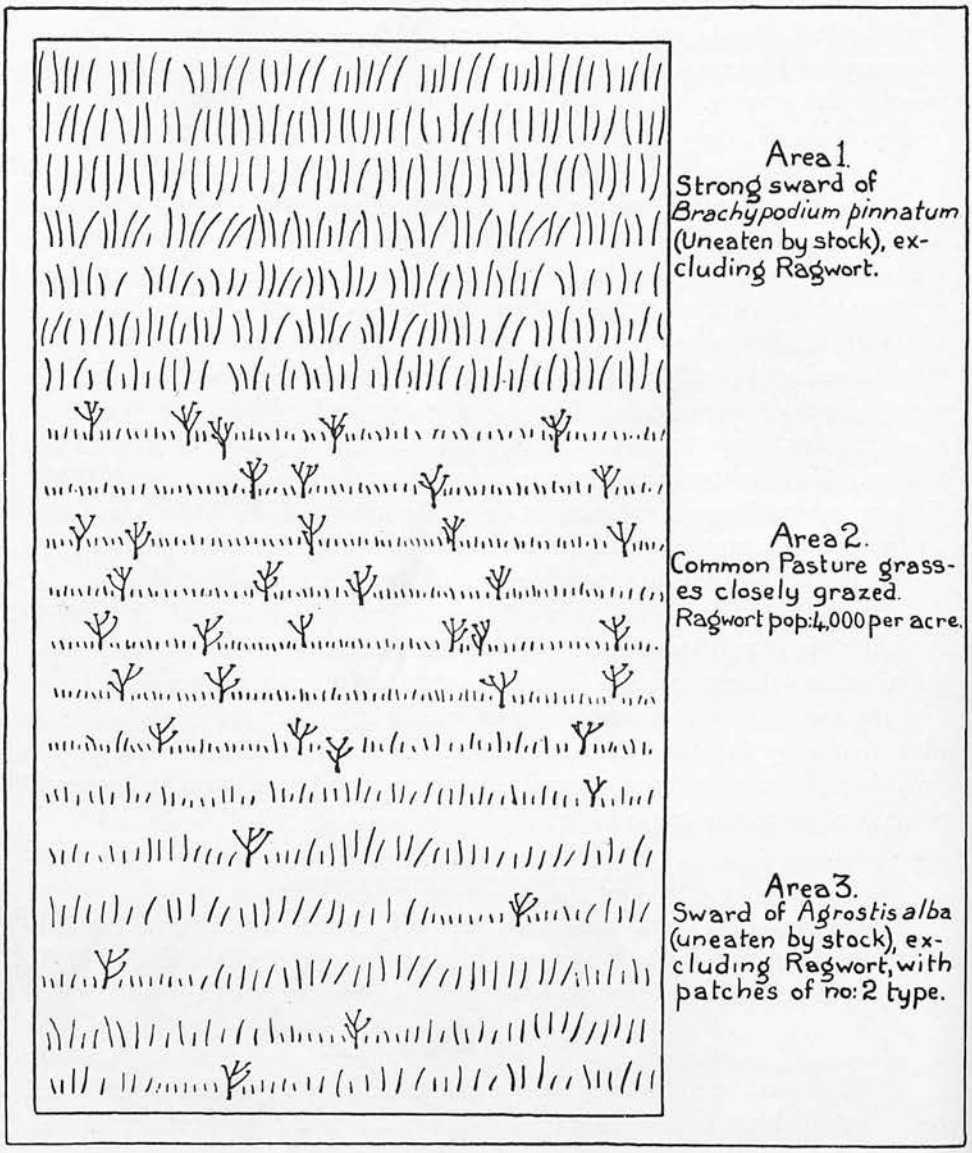


FIG. 2. Illustrating the effect of close grazing on the establishment of ragwort, and of thick sward on the exclusion of the weed. (Area of field, 30 acres.)

per acre. Area 3 was not so overgrazed and bore large quantities of *Agrostis alba*, which was not eaten by the stock. Where it grew thickly it practically excluded ragwort. In certain places the soil was exposed and herbage of the number 2 type with ragwort occurred. The two grasses, *Brachypodium pinnatum*

and *Agrostis alba*, which were so effective in excluding ragwort, were probably not greatly relished by the stock. Nevertheless, the effect produced by them indicates the importance of rank herbage and the necessity of avoiding overgrazing in ragwort control.

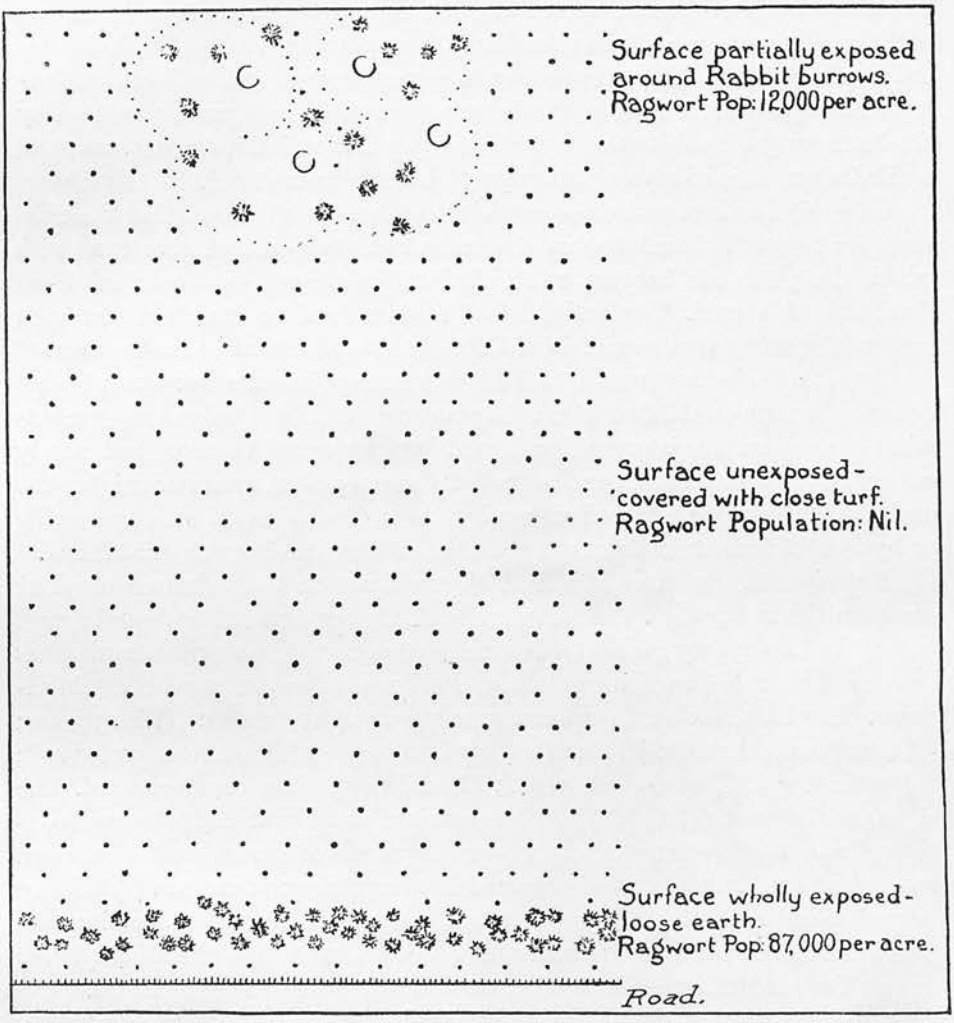


FIG. 3. Illustrating the effect of exposed soil surface on the establishment of ragwort seedlings.

To this positive evidence of the value of a good sward, we may add evidence, which although negative is corroborative. If strong grass competition excludes ragwort from the composition of the pasture, the entire absence of competition should greatly encourage the establishment of the weed. The following observations from Buckenham, Norfolk, endorse this statement: An area by the roadside, 150 yards long and about 2 ft. wide, consisting of loose soil thrown up by the roadmen, had a population of two

ragwort rosettes per square foot, or 87,000 per acre. Immediately within this strip *the land was covered with a close continuous turf in which there was no ragwort.* Still further in, about 90 yards from the road, this turf was riddled with rabbit burrows. An area measuring 12 ft. by 7 ft. (84 sq. ft.) surrounding four large burrows was examined and the following data obtained: mature ragwort plants on area 22; rosettes 21; mature plants per acre 12,000. In this area we have thus three zones; one where grass competition is absent and the ragwort population is 87,000 per acre; another where it is greatly reduced by the burrowing of rabbits and the ragwort population is 12,000 per acre; and a third where it is so severe that ragwort is entirely excluded.

Other similar areas were observed in Norfolk. It is evident that the chief cause of ragwort abundance in that county is the comparative ease with which the plant can become established in the open plant communities of derelict arable land. The activities of rabbits tend to maintain the open community and provide suitable *nidi* for the establishment of the ragwort.

From these observations in the field, two main points emerge: first, ragwort does not become established where the plant community is unbroken—such as when the soil surface is covered with rank herbage or with a short and closely grazed but continuous turf; and secondly, where the plant community is broken and the soil surface exposed either by the action of rabbits in burrowing or by that of farm animals in overgrazing, ragwort can become established.

Experiments. So much for field observations on the influence of plant communities on ragwort. The following confirmatory experiments were carried out in the Laboratory garden to determine the effect of rank grass, rank grass cut down, short but continuous turf, and of bare surface on ragwort establishment. Six plots, each 1 ft. square, were prepared as follows: (1) long grass; (2) long grass cut short; (3) short but continuous turf; (4) hard compacted soil; (5) ordinary tilth, seeds uncovered; (6) ordinary tilth, seeds covered. The difference between (2) and (3) may be explained as follows: in (2) the grass consists of short single stems with consequent tiny areas of exposed soil in between, somewhat similar to the effect obtained in overgrazing; whereas in (3) tillering or multiplication of stems has taken place, and instead of single stems there are small clusters or tufts of stems, forming a continuous mat which completely covers the soil surface—this is what we find in a well-managed pasture.

On each of these six plots, one hundred ragwort seeds were evenly distributed (viability of the seeds 80 per cent.). On examination one to two months later, the following numbers of seedlings were found: plot 1, no seedlings; plot 2, two seedlings; plot 3, no seedlings; plot 4, twenty seedlings; plot 5, fifty-three seedlings; plot 6, fifty-five seedlings.

An analysis of these figures shows that long grass in plot 1 and short but continuous turf in plot 3 completely excluded ragwort. What the exact causes of non-establishment were, whether the seeds could not germinate in plot 1 through the absence of light, or in plot 3 through insufficient moisture, or

whether in the event of germination the low light intensity suppressed the seedling, was not determined. However, the main point is that the observations made in the field—that long grass and short continuous turf effectively exclude ragwort—are confirmed by the results obtained from plots 1 and 3. In plot 2 a few seedlings became established in the exposed soil between the single stems—this supports the field observations on the effect of overgrazing on the establishment of ragwort; in plot 4, where the ground was hard, the seedlings were younger and of varying sizes and ages. Establishment appeared to have taken place where the ground was penetrated and softened at points by rain and worm casts; the physical condition of the soil may have increased the number of seedlings in this plot. In plots 5 and 6 a large number of seedlings were obtained, and it did not seem to make any difference whether the seeds were covered or not.

From this experiment we may infer that if a large amount of seed (about 100 per square foot) settled on four different types of field, it is possible for seedlings to arise in the following proportions:

On long grass	No ragwort seedlings per acre
On short but continuous turf ...	No ragwort seedlings per acre
On overgrazed pasture	86,120 ragwort seedlings per acre
On hard exposed soil	871,200 ragwort seedlings per acre
On open soil	2,308,680 ragwort seedlings per acre

These figures are endorsed by field observations. Of course, a uniform covering of 100 seeds per square foot is never obtained, and, if it were, a very large number of seedlings arising from such a dense covering would succumb in the intraspecific competition. The results of the experiment agree with the evidence from the natural areas at Hambledon and Buckenham.

It is evident then from these experiments and observations, that when considering ways and means for the natural control of ragwort, the condition of the pasture is of the greatest importance and must not be neglected. Good farming, good range management, and ragwort abundance are incompatible. Many of the dairy farms of New Zealand, which are heavily infested with the weed, exhibit evidences of extensive overgrazing, and this state of affairs must be remedied before ragwort can be brought appreciably under control.

(β) Zoological.

The chief zoological factors influencing ragwort in this country are four in number: man, sheep, rabbits, and insects.

(*a*) *Man, rabbits and sheep.*

The influence of *man* may be direct, as in measures explicitly directed to the extirpation of the weed, or indirect, as in the conduct of farming operations not specifically directed against ragwort, but resulting in conditions such as those described in the preceding section, which are, in fact, unfavourable to it.

The effect exerted by *rabbits* in burrowing has already been mentioned. When dealing with the effect of exposed soil on the establishment of ragwort, it was pointed out that the areas immediately surrounding the rabbit burrows in the light, sandy soil of Norfolk, are suitable seed beds for the weed. As well as this open burrowing on large stretches of the desolate East Anglian heaths and other regions, an additional effect favourable to ragwort establishment is produced by their close-grazing activities. A large field at Medmenham, Bucks, is a case in point. This field was surrounded by a wood, from which large numbers of rabbits emerged and closely cropped the sward of the fringe and for some distance inwards. Bare patches were exposed and ragwort from the neighbouring badly infested waste lands colonised the area to the extent of 580 plants per acre. (Pl. XX.)

The action of rabbits is thus, in general, distinctly favourable to the increase of ragwort. They do eat the plant, but only sparingly, and not enough to check it.

Sheep, on the other hand, are effective controlling agencies. They are very fond of ragwort, especially in the rosette stage, and are relatively little affected by its toxic principles.

(*b*) *The insects recorded from ragwort.*

The three biotic factors affecting ragwort that have been mentioned in the preceding paragraphs are, of course, already present in New Zealand. But the insect enemies of the plant in Europe were not introduced with it into its new home, and are thus of particular interest from the economic standpoint.

A number of insects from each of the following five orders: Lepidoptera, Diptera, Coleoptera, Hemiptera, and Thysanoptera, have been recorded from ragwort. (The figures refer to the month of the year.)

(i) Lepidoptera.

Arctiidae.

(1) *Tyria jacobaeae* L.: moth 5, 6; larva 7, 8. Larvae attack flower-heads, leaves and stem. Britain north to Caledonian Canal, Europe to West Central Asia. Other host: *Senecio vulgaris*.

(2) *Arctia villica* L.: moth 6; larva 8–5; larvae attack leaves. England, Roxburgh, local, Europe to Turkestan. Other hosts: *Myosotis*, *Plantago*, *Rumex*, etc.

(3) *Arctia fuliginosa* Bd.: record.

Caradrinidae.

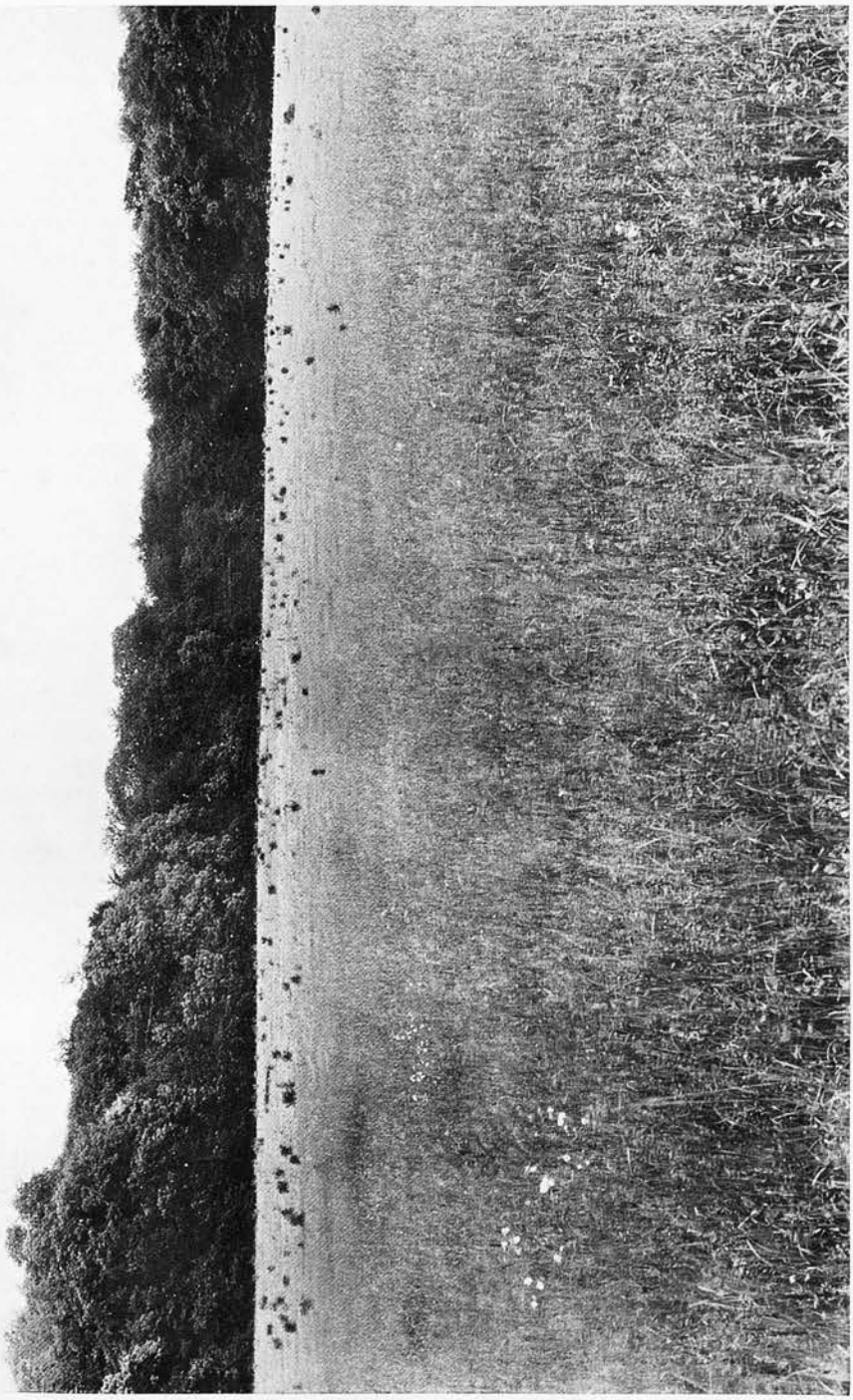
(4) *Hadena meticulosa* L.: moth 5, 6, 9, 10; larva 7, 8, 10–3. Britain to Shetlands, Ireland, common, Europe to Syria, Northern Africa. Other hosts: *Rumex*, *Viola*, etc.

(5) *Aporophyla* (*Epunda*) *lutulenta* Borkh.: moth 9; larva 10–4. Britain to Orkneys, Ireland, local, Europe. Other hosts: *Myosotis*, *Lithospermum*, *Achillea*, etc.

(6) *Polia lichenea* Hubn.: moth 8, 9; larva 11–5. Western England to Lancashire, Kent, Sussex, Yorkshire, Eastern Ireland, local. Other hosts: *Scabiosa*, *Rumex*, etc.

(7) *Agrotis* (*Pachnobia*) *simulans* (*pyrophila*): record.

(8) *Ochria* (*Gortyna*) *ochracea* Hubn. (*flavago* Esp.): moth 8, 9; larva 5–8. In stems. Britain to Caledonian Canal, Ireland, rather local, Central Europe to Western Siberia. Other hosts: *Carduus*, *Arctium*, *Verbascum*, etc.



Phot. 1. Showing the effect of rabbits on Ragwort establishment. In the background a strong Ragwort colony has become established as a result of lowered grass competition, following on the close grazing action of numerous rabbits. The strong sward in the foreground, untouched by rabbits, has excluded the weed.

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Plusiidae.

(9) *Plusia iota* L.: moth 6, 7; larva 8–5. Britain to Orkneys, Ireland, common, Northern and Central Europe to Western Turkestan. Other hosts: *Lamium*, *Urtica*, etc.

Hydriomenidae.

(10) *Eupithecia absinthiata* Clerck.: moth 6, 7; larva 8–10. On flowers. Britain to Ross-shire, Ireland, common. Northern and Central Europe to Eastern Siberia. Other hosts: *Artemisia*, *Achillea*, etc.

(11) *Eupithecia pimpinellata* Hubn. (*denotata* Guen.): moth 4, 5, 8; larva 6, 9, 10. England to Yorkshire, Eastern Ireland, Northern and Central Europe to Western Siberia. Other hosts: *Pimpinella*, *Achillea*, etc.

(12) *Eupithecia vulgata* Haw.: moth 5, 6; larva 7. Britain to Hebrides, Ireland, very common, Northern and Central Europe to Eastern Siberia. Other hosts: *Rubus*, etc.

(13) *Eupithecia oblongata* Thunb. (*centaureata* Fabr.): moth 5, 6, 8; larva 7, 9. Britain to Caledonian Canal, Western Ireland, common, Central and Southern Europe to Western Turkestan. On flowers and seeds of many Umbelliferae and Compositae.

(14) *Eupithecia castigata* Hubn. (*jasioneata* Crewe): moth 5, 6; larva 8, 9. Britain to Hebrides, Ireland, common, Europe to Eastern Siberia. Other hosts: *Scabiosa*, *Lychnis*, *Ononis*, *Epilobium*, etc.

(15) *Eupithecia virgaureata* Doubl. (*pimpinellata* Guen.): moth 5, 6; larva 8, 9. On flowers. England to Yorkshire, Ireland, local, Northern and Central Europe to Eastern Siberia. Other hosts: *Solidago*, etc.

(16) *Eupithecia expallidata* Doubl.: moth 7, 8; larva 9. On flowers. Southern and Western England to Lancashire, Aberdeen, Ireland, local. Central Europe. Other host: *Solidago virgaurea*.

(17) *Eupithecia* (*minutata* Guen.) *goossensiata* Mab.: moth 6, 7; larva 8–10. Britain to Orkneys, Ireland, common, Northern and Central Europe. Other hosts: *Erica*, *Calluna*, *Scabiosa*.

Phycitidae.

(18) *Homeosoma cretacella* Rossl. (*senecionis* Vaughan): moth 5, 7; larva 6, 8, 9. In flower heads and stems. Southern England to Gloucester and Norfolk, on coasts, local, Holland, Germany, Siberia.

(19) *Homeosoma nimbella* Zell. (*saxicola* Vaughan): moth 6, 8; larva 7, 9. On flowers. Britain to Kirkcudbright, Eastern Ireland, on coasts, local, Europe to Palestine. Other hosts: *Anthemis*, *Jasione*, etc.

(20) *Homeosoma nebulella* Hubn.: moth 7, 8; larva 8, 9. On flowers. England to Yorkshire, rather common, Europe to Turkestan. Other hosts: *Carduus*, etc.

Pyraustidae.

(21) *Pyrausta alpinalis* Schiff.: moth 7, 8; larva 6. Amongst spun leaves. Clyde to Ross-shire, Northern Ireland (Antrim), mountains of Central Europe and Central Asia.

Phaloniadae.

(22) *Phalonia atricapitana* Steph.: moth 5, 6, 8; larva 7, 9–4. On flowers and stems. England, Roxburgh, Ireland, local, Central Europe to Siberia.

(23) *Phalonia dubitana* Hubn.: moth 6, 8; larva 7, 9. In seeds. Britain to Clyde, Northern Ireland, local, Northern and Central Europe to Siberia. Other hosts: *Crepis*, *Solidago*, etc.

(24) *Euxanthis aeneana* Hubn.: moth 6; larva 9–4. In stems and roots. Kent, Sussex, Surrey, Middlesex, Essex, local, West Central Europe. Other host: *Senecio paludosus*.

Eucosmidae.

(25) *Eucosma nigromaculana* Haw.: moth 6, 7; larva 9. In seeds. Britain to Clyde, Ireland, local, Central Europe.

(26) *Eucosma trigeminana* Steph.: moth 6, 7; larva 9–12. In roots. Britain to Sutherland, Eastern and Southern Ireland, rather local, Central Europe.

Coleophoridae.

(27) *Coleophora tricolor* Wals.: moth 7, 8. Sussex, Norfolk, local. Other hosts: *Triticum*, etc.

Records of Lepidoptera mostly from Meyrick, *British Lepidoptera*.

(ii) DIPTERA.

Cecidomyiidae.

(28) *Stictodiplosis jacobaeae* H. Loew. Attacks flowers and seeds, causing capitula to be strongly swollen and tinted red at base. Larvae gregarious. Records from all English counties except Cumberland. Recorded from *S. erucifolius* once in Co. Durham.

(29) *Cecidomyid* sp.: on ragwort and *S. aquaticus*. Several records from Northumberland and Durham.

Agromyzidae.

(30) *Agromyza aeneiventris* Fln.: larvae bore in stems.

(31) *Phytomyza albiceps* Meig.: larvae mine leaves. In leaves from June onwards. Common in Europe and America. Other hosts: *Chrysanthemum*, *Aconitum*, etc.

(32) *Phytomyza geniculata* Macq.: as *albiceps*. Europe.

Trypetidae.

(33) *Sphenella marginata* Fln.: larvae attack capitulum, causing feeble swelling at base. Solitary.

(34) *Ensina sonchi* L.: single male bred from flower heads by Richards.

Anthomyiidae.

(35) *Pegohylemyia jacobaeae* Hardy: adults emerge towards end of June. Larvae in capitula July–August.

(36) *Pegohylemyia seneciella* Meade: as *jacobaeae*.

(iii) COLEOPTERA.

Phytophaga: Halticae.

(37) *Longitarsus dorsalis* F.: on *Senecio jacobaea* and *S. vulgaris*. Locally common in Isle of Wight, Ventnor, etc., London district, local and not common. Adult hibernates. Comes out about May; eggs, larvae and pupae follow between then and October, when a new generation emerges to hibernate as adults.

(38) *Longitarsus piciceps* Steph.: on *Senecio jacobaea*. Very local but common where it occurs. Darenth Wood, Chatham, Northumberland district, etc. Life history as *dorsalis*.

(39) *Longitarsus jacobaeae* Wat.: on *Senecio jacobaea*. Common and generally distributed throughout the greater part of the country. Imago, end of July to August. Full grown larva, June. Larvae of these beetles feed openly on the roots. The adults feed on the leaves.

(40) *Longitarsus gracilis* Kuts.

(41) *L. suturellis* Dup. (*thoracicus* Steph.); and

(42) *L. ochroleucus* Marsh., are also recorded from ragwort.

Records of Coleoptera from Fowler, *Coleoptera of British Isles*, etc.

(iv) HEMIPTERA.

Pentatomidae.

(43) *Pentatoma rufipes* L.: imago, end of June to October. On flowers of ragwort. General throughout British Isles. Other hosts: *Quercus*, *Crataegus*, *Fraxinus*, etc.

Coreidae.

(44) *Therapha hyoscyami* L.: imago, August–September. Swept from flowers. Near Pendine, near sea. Other hosts: *Ononis*, *Erodium*, *Hyoscyamus*, etc.

Berytidae.

(45) *Berytus signoreti* Fieb.: imago, March–October. From roots. Northumberland—Gloucester, Herts, Surrey, Berks, etc. Other host: *Erica tetralix*.

Tingidae.

(46) *Monanthia ciliata* Fieb.: imago, April–June. Under ragwort in sandy places. Oxon, Berks. Other hosts: *Ajuga reptans*, *Verbascum*, etc.

(47) *Monanthia simplex* H.S.: imago, May–August. Bucks, Kent, Surrey, Hants, Devon. Also under *Euphorbia cyparissias*.

Capsidae.

(48) *Phytocoris ulmi* L.: imago, June–October. All over Europe. Other hosts: *Ulmus*, *Prunus*, *Betula*, *Acer*, *Alnus*, etc.

(49) *Calocoris bipunctatis* Fabr.: imago, June–October. All over Europe. Other hosts: *Vicia sativa*, *Carduus*, *Papaver*, etc.

(50) *Neocoris bohemani* Fall.: imago, July–August. Cheshire, Kent, Devon, and nearly whole of Europe. Other host: Sallow. On thistle and ragwort, probably casual occurrences.

Coccidae.

(51) *Targiona nigra*: at base of woody stem. France, Corsica, Italy, Algeria, etc. Other hosts: *Cineraria maritima*, *Fagonia cretica*, *Genista delphinensis*, etc.

Aphididae.

(52) *Aphis rumicis* L.: June–July onwards. Europe generally, Africa, India, etc. Forty-seven other hosts (*Artemisia*, *Carduus*, *Pyrus*, etc.).

(53) *Aphis jacobaeae* Schrk.: common June and July. Wye, Herne Bay, Germany, Belgium, etc.

(54) *Anuraphis cardui* L.: July–September. General over England and Wales, Europe, America. Other hosts: *Carduus* spp., *Senecio* spp., *Chrysanthemum*, etc.

(55) *Anuraphis helichrysi* Kalt.: June–Autumn. Great Britain, Ireland, Europe, etc. Other hosts: plum, damson, etc.

Records of Hemiptera mostly from Butler, *Hemiptera-Heteroptera*.

(v) THYSANOPTERA.

Thrinoidea.

(56) *Haplothrips distinguendus* Uzel.: adults from end of June to October. Eggs laid amongst flowers. North-east Scotland and Southern England, etc. Ragwort true host plant.

At least twenty-one other species of Thysanoptera are found on ragwort, many of which are merely casual visitors, while others may breed on the plant, although they have many other hosts, and yet others may occur in great numbers on the weed but do not breed on it. Among the latter are *Physothrips atratus* Hal., *P. vulgatissimus* Hal., *Thrips flavus* Schrank. and *Thrips fuscipennis* Hal. The occasional breeders on ragwort are *Aelothrips fasciatus* L., *Aptinothrips rufus* Gmelin var. *stylifera* Trybom and *Thrips tabaci* Lindeman.

After a preliminary survey, taking into account the effective damage produced by the various species and the specificity of their food habits, two insects were selected for special study; the Ragwort Moth or Cinnabar (*Tyria jacobaeae*), belonging to the family Arctiidae, and the Anthomyiid fly, *Pegohylemyia seneciella* Meade.

Several other species, which do minor damage to ragwort, have also received some study. Among these may be mentioned *Agromyza aeneiventris* Fln., a

dipterous stem borer, *Homeosoma nimbella* Dup., a lepidopterous stem borer, *Phytomyza atricornis* Mg. and *Spilographa zoe* Loew., leaf-miners, and an aphid, *Aphis jacobaeae* Schrk.

(*c*) *The two important insects.*

A. Tyria jacobaeae *L.*

(i) *Synonymy, description, and distribution.*

Tyria (*Hipocrita, Euchelia, Callimorpha*) *jacobaeae* L. is a member of the family Arctiidae (Lepidoptera). Meyrick describes it in *British Lepidoptera* as follows:

"Head, thorax, and abdomen black. Forewings blackish grey; a crimson subcostal streak from base to $\frac{5}{6}$, extremity expanded; a crimson dorsal streak from base to $\frac{2}{3}$; a crimson dorsal spot below the apex, and another above the tornus. Hindwings crimson; a costal streak, middle of terminal edge, and cilia blackish grey. Wing spread 35–45 mm."

The species occurs commonly throughout Britain, its range extending as far north as the Caledonian Canal, although it is scarce north of the Clyde. It is also common in Ireland. In Europe it occurs as far east as, and including West Central Asia.

(ii) *Life history.*

The adult. In England the moths emerge from the hibernating pupae about mid-May, and become more plentiful throughout the latter half of May and June. The eggs are laid on the under-surface of the leaves of *Senecio jacobaea* L., and occasionally on *S. vulgaris* L. (groundsel), to which two plants the species is confined in nature. In tests, the larvae have also been found to feed on *S. cineraria*, the garden cineraria. The eggs are deposited on the under-surfaces of the lower leaves of ragwort, in clusters, containing from one to 130 or more, though the clusters usually contain from thirty-five to forty-five eggs. Occasionally there may be more than one cluster on a leaf. The eggs, which measure 0·65 mm. in diameter, are yellow, and faintly reticulated. Before hatching, the chorion, through which the black cuticle of the larval head can easily be seen, changes from yellow to a glistening greyish colour. In the field incubation requires approximately 13 days, while in the incubator, at a temperature of 23° C., the eggs hatch in 5 days. The average number of eggs laid by a female is about 200, the lowest number laid by those under observation being ninety-eight, and the highest 301. In one case observed, oviposition proceeded as follows:

Moth paired on 13th June, 1930.

14th June, 1930	...	29 eggs laid
16th June, 1930	...	181 eggs laid
19th June, 1930	...	91 eggs laid
	Total	301

The larva. The eggs hatch out about the end of May, or later, according to the season, and larvae are common throughout June and the greater part of July, except in a late season like 1932, when they were scarce until the end

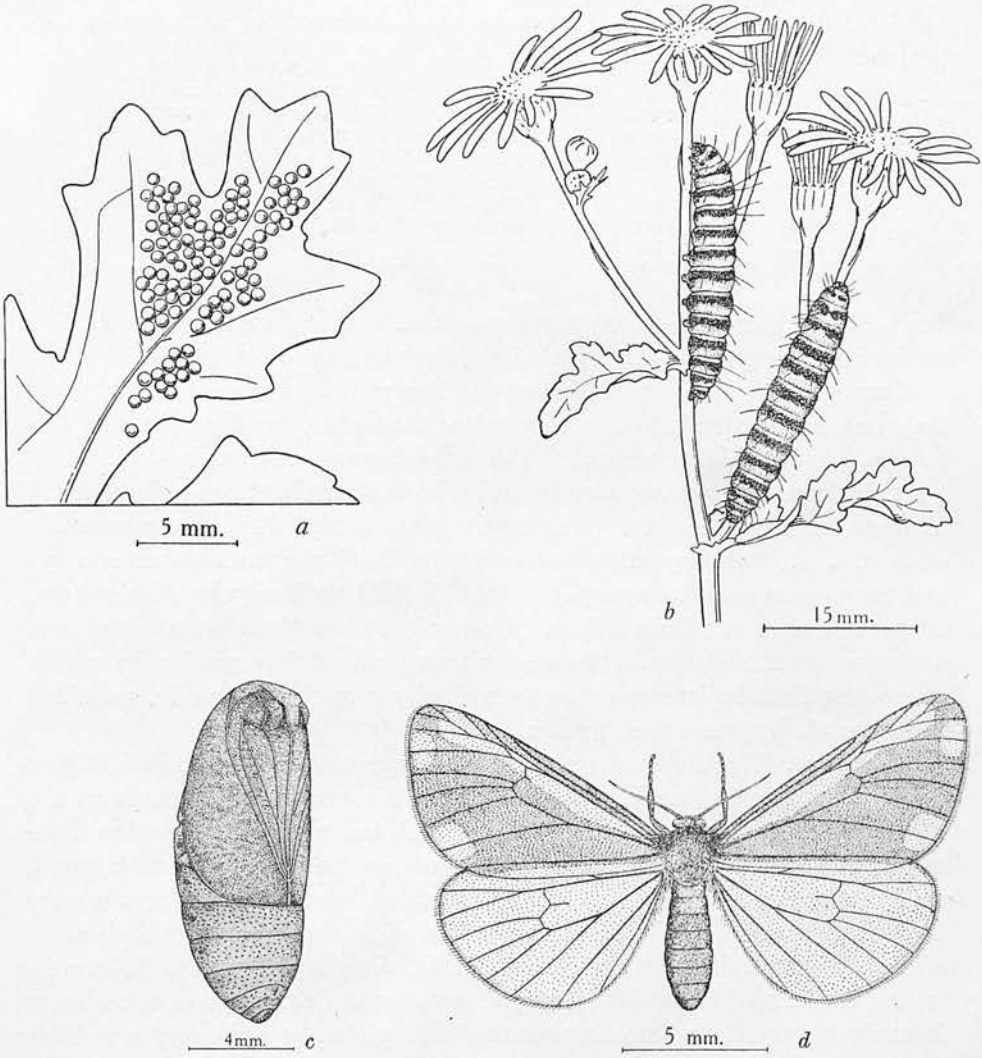

FIG. 4. *Tyria jacobaeae* L.: *a*, eggs on under side of ragwort leaf; *b*, larvae; *c*, pupa; *d*, adult with wing venation emphasised.

of June. Towards the end of July they prepare to enter the pupal stage. There are five larval stadia. The first instar is greenish yellow in colour, with an arrangement of black dots on the tip of the hair papillae. On the third day after hatching, the general effect is deep yellow with black dots. The second instar, which appears 5–6 days after hatching, is striped, black bands alternating

with narrower bands of a greyish green colour. After 3–4 days in this instar the ground colour becomes yellow, with a regular arrangement of black dots. About the tenth day after hatching the larva enters the third stadium, when it assumes the characteristic yellow and black bands of the two remaining stages.

The following table gives the various measurements of each instar, and the length of each stadium:

Instar	Length mm.	Breadth at middle mm.	Breadth of head mm.	Length of stadium days
1	2·09	0·45	0·385	5–6
2	4·00	0·75	0·600	5–6
3	8·00	1·30	0·942	5
4	13·00	2·20	1·430	5
5	15·50	3·70	2·010	10–11
Mature 5	25·00	5·00	2·010	—

The larval period occupies just over one month. The head measurements in the successive stages agree with Dyar's Law, the mean ratio being 1·51.

During June and July, in the south of England, the larvae of the cinnabar may be seen in certain areas in countless thousands, rapidly eating up the flowers, leaves, and top parts of the stems of ragwort. At Henley-on-Thames a ragwort area had a population of twelve larvae per plant, or nearly one and a quarter millions per acre. Over large regions in Norfolk they were equally abundant. In fact they are a feature of the Breckland area of this county, and are so numerous in some parts that they find their way into the cottars' houses in search of suitable places for pupation. Sometimes a road intersects a ragwort area, and the larvae, or canker-worms as they are locally called, in crossing from depleted ragwort to fresh plants on the other side, get killed in thousands by passing motor cars.

The pupa. The insect enters the pupal stage towards the end of July or a few weeks later, according to the season. A few odd larvae remain on the plants for several weeks after the main batch has pupated. When the fifth-stage larva is fully fed, it seeks out some protected position under moss, grass, small stones, or just beneath the soil surface. Here it may form a very imperfect cocoon with the aid of soil and a slight webbing, but this is often absent. When the last larval skin is moulted, a bright yellow pupa is formed, which, if touched, is capable of slight movement. In the course of 24 hours it hardens, the colour becoming reddish, and gradually darkening to reddish brown. In this stage the insect passes the winter.

In length, the pupa measures about 11·5 mm., while at its middle it is 5 mm. broad.

Testing of Tyria. An extensive series of larval tests was carried out in order to find out if *Tyria* can attack other plants. The selected plants were lettuce, chrysanthemum, sunflower, golden rod, aster, Michaelmas daisy, and dahlia. Negative results were obtained, none of these plants being eaten by the larvae. This part of the work was carried out at Rothamsted by Mr J. C. F. Newton.

(iii) *Parasites of the eggs and larvae.*

The following parasites of *Tyria jacobaeae* L. are recorded in the literature. Those of which the names are in brackets have not been reared by me, and are probably extremely rare:

HYMENOPTERA.

Braconidae:

1. Apanteles popularis Haliday.
2. (Apanteles difficilis Nees.)

Ichneumonidae:

3. (Ichneumon (Cratichneumon) Gravenhorsti Fnsc.)
4. (Melanichneumon saturatorius Thoms.)
5. (Mesostenus obnoxius Grav.)
6. (Spilocryptus incubitor Strom.)
7. (Spilocryptus migrator Fab.)
8. (Cryptus obscurus Grav.)
9. (Erigorgus insidiator Forst.)
10. (Labrorhychus tenuicornis Grav.)
11. (Exetastes illusor Gr.)
12. Mesochorus facialis Bridg.
13. (Mesochorus anomalus Holmgr.)
14. (Hemiteles fulvipes Grav.)

} Hyperparasites of Apanteles popularis

DIPTERA.

Tachinidae:

15. (Tachina macrocera Rob. Desv.) (Tachina nitidiventris Zett.)

Very few of these parasites were obtained from English material, though an immense number of *Tyria* larvae and pupae were reared. On the other hand, several new parasites were reared, and added to the list.

Egg parasites. Although very many thousands of eggs were collected in the Farnham Royal area and allowed to hatch, no parasites were obtained. A number of eggs were exposed to attack by the Chalcid egg parasite *Trichogramma* sp., which has many lepidopterous hosts, but negative results were obtained. One per cent. of the eggs collected in the field were sterile.

Parasites of the larvae. (1) *Apanteles popularis* Hal.—Braconidae (Microgasteridae). During 1930, 1931, and 1932, several thousand *Tyria* larvae from different areas in Buckinghamshire, Oxfordshire, Surrey, and Norfolk, were dissected for parasites. The first and second stage endoparasitic larvae of this Braconid, with the characteristic caudal vesicle, were obtained in the following numbers: 1930, 4 per cent.; 1931, 5 per cent., one area in Surrey—Wentworth—had 19 per cent.); 1932, 41 per cent. This variation in the percentage of parasitism from year to year was also noted by Lyle, who in one year found a 60 per cent. attack, and in the following year, in the same area, no attack. Daviault, in 1928, found that 40 per cent. of the caterpillars were attacked by *A. popularis* in the sand-dunes at Wimereux, near Boulogne.

This parasite is gregarious, several larvae inhabiting a single *Tyria* caterpillar. The highest number found was fifteen, while the average was five. The adults emerge from their cocoons during the first weeks of July, and proceed to parasitise the early stages of the *Tyria* caterpillars. The larva, when fully fed (towards the end of July), emerges from the mature fifth stage *Tyria* caterpillar, and hibernates inside a tough, woolly, white cocoon, pupating

shortly before the appearance of the imago. The cocoons are arranged in irregular groups of 6–9, and are connected with each other by a few threads.

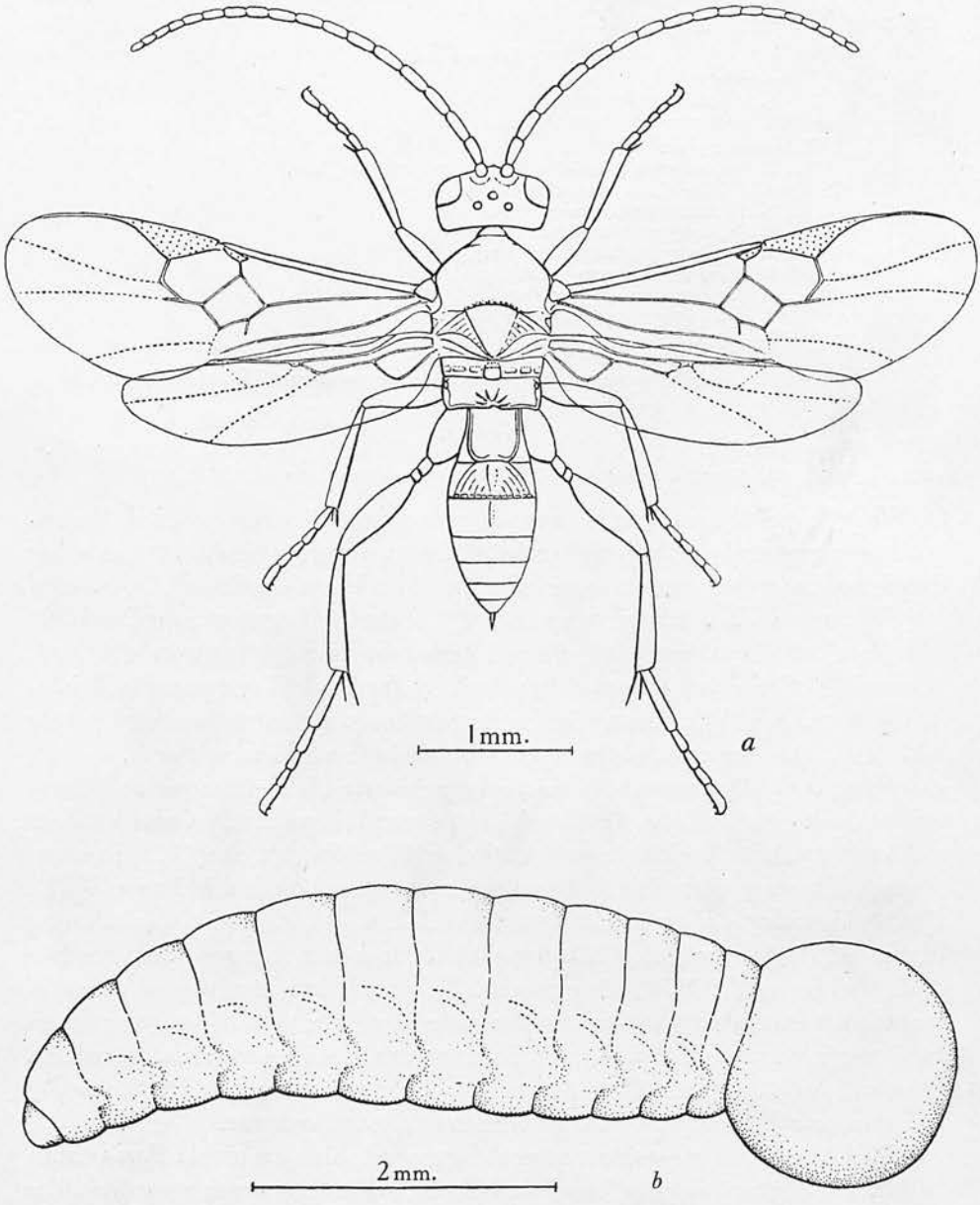

FIG. 5. *Apanteles popularis* Hal.: *a*, adult female; *b*, second stage larva.

A rather inadequate description of the biology and larval stages of this species has been given by Daviault.

(2) *Mesochorus facialis* Bridg.—Ichneumonidae (Ophioninae). The larvae of this hyperparasite were dissected from the last stage larvae of *Apanteles popularis* Hal., removed from living caterpillars of *Tyria* and found to occur in the following numbers: Buckinghamshire, 60 per cent.; Norfolk, 15 per cent. *Mesochorus* is a solitary parasite.

(iv) *Parasites and predators of the pupae.*

(1) *Ichneumon* (*Melanichneumon*) *perscrutator* Wsm. (Ichneumonidae—Ichneumoninae). Several thousand of the pupae of *Tyria jacobaeae* L., collected in large quantities from Norfolk during the seasons of 1929, 1930, 1931, were dissected in order to ascertain the percentage infestation by this solitary

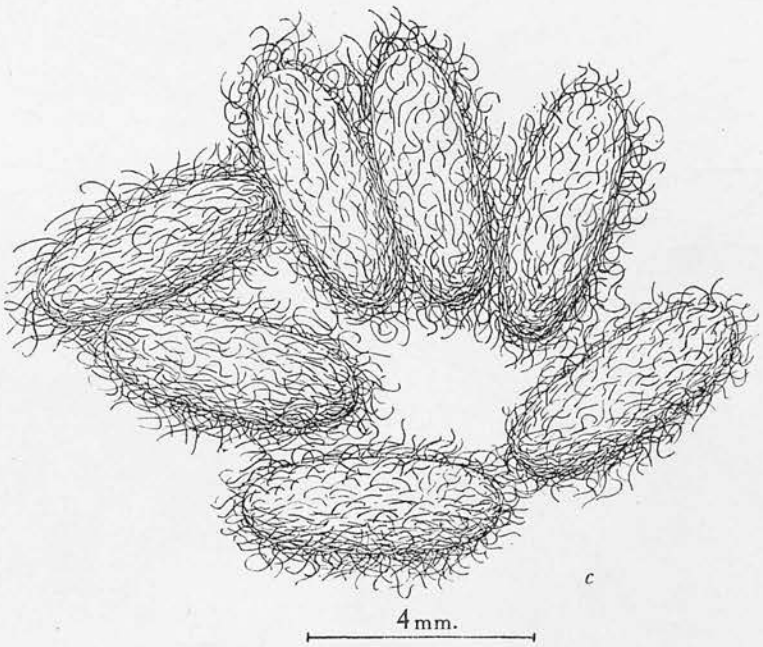

FIG. 5. *Apanteles popularis* Hal.: *c*, cocoons.

parasite. In 1929 this amounted to 15 per cent., but in the following years, 1930, and 1931, it fell to 2–3 per cent. This sudden drop might have been attributed in part to the large collection of 1929, with its accompanying reduction in the ichneumon population, were it not for the fact that the infestation outside the collecting areas was similarly 2–3 per cent. Other factors must therefore contribute to this violent fluctuation in the numbers of the parasite.

As far as I am aware this is the first rearing record of *Ichneumon perscrutator* Wsm.

(2) *Psychophagus* (*Diglochis*) *omnivorus* Walk. (Chalcidoidea—Pteromalidae). During the first collecting season (1929–30), the larvae of this parasite were obtained by dissections of the host, and the adults bred in large

numbers from *Tyria* pupae. Although very abundant, the actual loss which the *Tyria* population incurred as a result of its activities was relatively small—due to its superparasitic habit. As many as forty-four or more adults issued from a single *Tyria* pupa, while the average number of parasite larvae in an infected pupa was about thirty-two. The infestation in the main collection averaged 3–4 per cent. One lot of 200 pupae had fifty-four (or 27 per cent.) infested. In the two following collecting seasons (1930–1, 1931–2) the infestation by *Psychophagus* was practically nil.

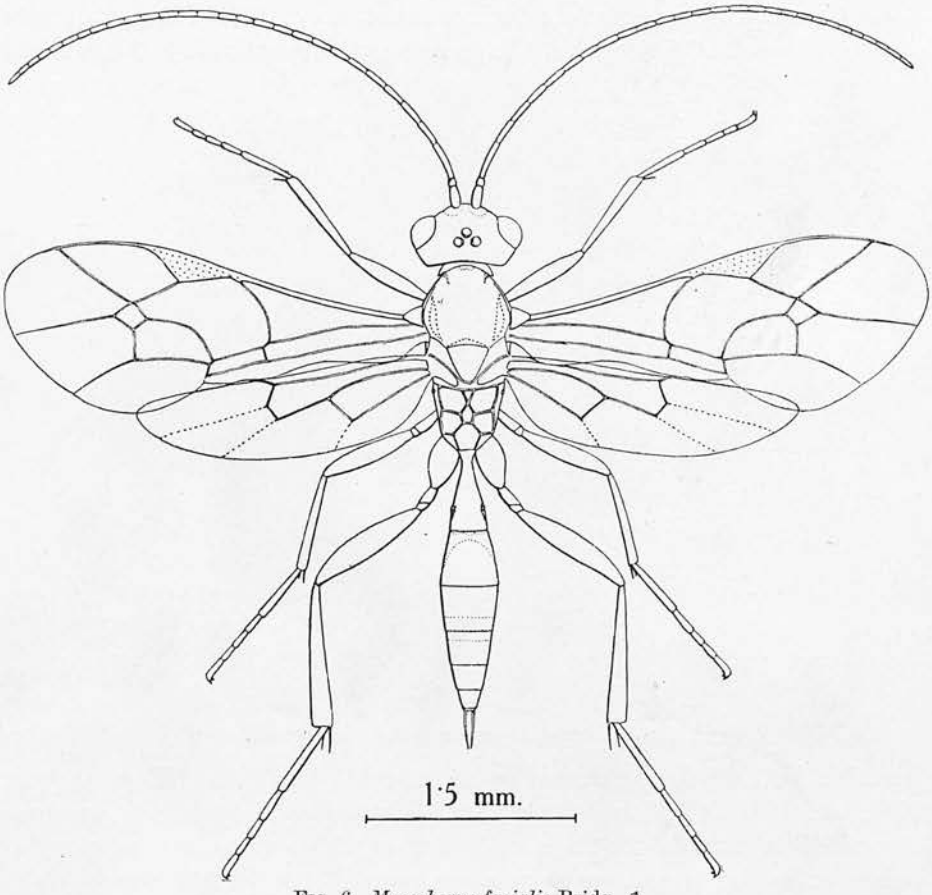

FIG. 6. *Mesochorus facialis* Bridg. ♂.

A few specimens of the following were also reared from *Tyria* pupae:

Ichneumonidae:
- Cryptinae: *Hemiteles* sp.
- Pimplinae: *Pimpla instigator* F.

Chalcidoidea:
- Chalcididae: *Brachymeria minuta* L.
- Pteromalidae: *Coelopisthia vitripennis* Thoms.

Fungus parasites of the pupae. The pupae of *Tyria jacobaeae* suffer rather heavily from the attack of various species of fungi. An attempt was made to isolate and identify each species. For this purpose two media were employed: potato-dextrose agar, and malt and meat extract. Both gave good results. Another method which did away with the necessity for cultivation media, consisted in taking a small piece out of the integument of each of a hundred pupae with a pair of forceps, sterilising the instrument in a flame after each

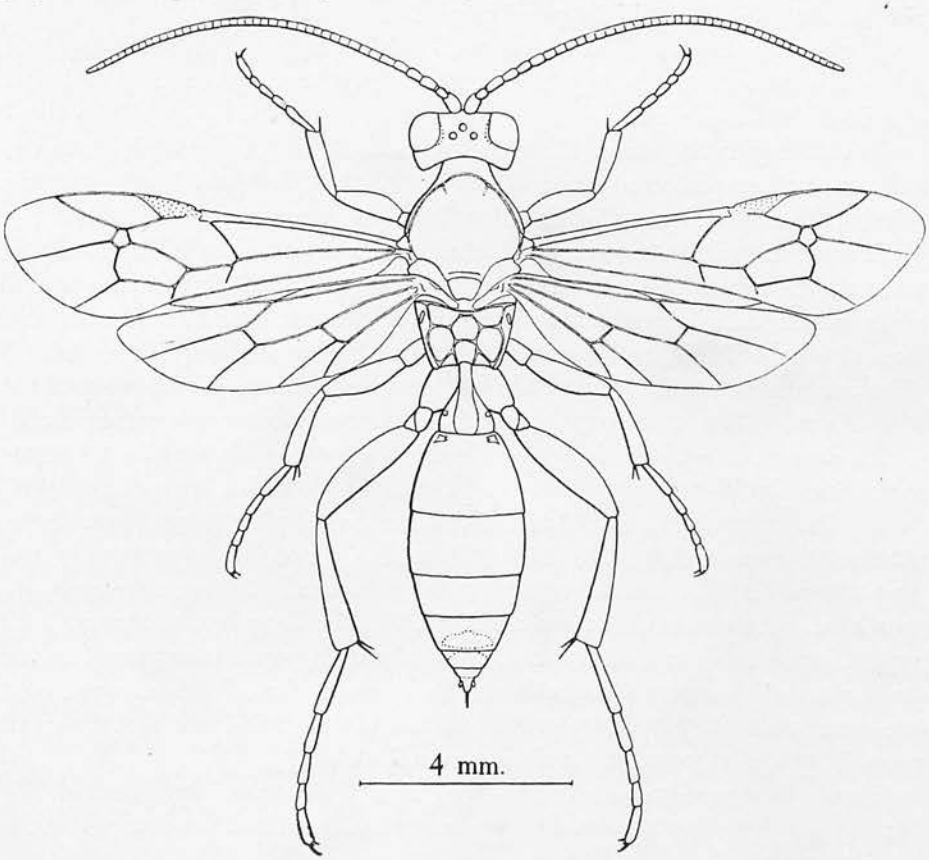

FIG. 7. *Ichneumon perscrutator* Wsm. ♀.

operation. The pupae were then placed on a tray containing damp sterilised sand or moss, and the whole covered with a bell-jar. Under such ideal conditions, any fungi present in the pupae soon grew out of the openings and were then ready for identification.

Towards the end of the 1930–1 period, the following fungi were isolated and identified, from pupae collected at Stanford, Norfolk:

Isaria farinosa	Infestation ...	10·5 per cent.
Fusarium sp.	Infestation ...	7·7 per cent.
Beauveria Bassiana ...	Infestation ...	0·5 per cent.

Collections of pupae were made in the Norfolk area as opportunity offered throughout the pupal periods of 1929–30, 1930–1, and 1931–2. Several thousand dissections were made, and the average percentage mortality caused by the combined attack of these fungi ascertained. In 1929–30 this mortality was equal to 16 per cent. in the earlier part of the pupal period (August–May), increasing towards the end to 20–22 per cent.; in 1930–1, 5 per cent. in the earlier period, increasing to 19 per cent. in the later, and in 1931–2, 16–18 per cent. in the middle of the pupal period.

The results thus obtained show that *Tyria* in the pupal stage is subjected to an annual loss of 16–20 per cent. of its population from the combined attack of the fungi cited.

Predators of Tyria *pupae.* Since the larvae of *Tyria* are distasteful to birds, and are further protected from attack by their yellow and black warning colours, the effect of predators is felt only in the pupal stage.

Several experiments were conducted during the winter of 1929–30, to ascertain the percentage of mortality in *Tyria* pupae, resulting from the action of predators. These experiments were made in Norfolk, over 100 miles distant from the Laboratory, consequently they were rather limited. Nevertheless, although general conclusions cannot be drawn from them, they serve to show that the mortality in the pupal stage from various predators is considerable.

An area in Breckland, in which the natural population was found to be approximately 25 pupae per 100 sq. ft., and which had a large quantity of denuded ragwort stems, was chosen and a number of plots pegged out. Three of the plots measured 10 ft. by 10 ft. (100 sq. ft.). In each of these twenty-five pupae were placed in small groups under stones, simulating, as closely as possible, the natural position and numbers. Two further plots, measuring 1 ft. by 1 ft., were made in a mossy area, and forty-eight pupae were placed under the surface of the moss at equal intervals in each. Near these, on open soil, two exactly similar plots were prepared, and pupae, at the rate of forty-eight per plot, placed at equal intervals on the soil surface.

These plots were prepared about the end of October and examined at the beginning of December, about five weeks later. The mortalities observed were as follows:

Mortality in the plots with pupae under stones	...	65 per cent.
Mortality in the plots with pupae under moss	...	69 per cent.
Mortality in the plots with pupae on soil surface	...	90 per cent.

The experiments thus indicate that the effect of predators in reducing the numbers of *Tyria* in the pupal stage is very great. At least 60 per cent. were accounted for in this manner in the area under review—Stanford, Norfolk. The pupae occur most generally under moss and small flat stones, which are abundant in Breckland. Very occasionally they may be found on the soil surface.

Observation and experiment indicate that the following animals may be listed as probable predators: moles, mice, crows, rooks, and game birds. Fed to pheasants the pupae were eaten sparingly; partridges also ate them. The most important predator is probably the mole. In several plots mole runs were discovered under the stones where pupae had been placed, and from all these the pupae had disappeared. Again in certain areas, where *Tyria* was known to be pupating, the soil was riddled with mole runs, and in such areas pupae were very scarce, although there had been an abundant supply of larvae. Crows and rooks have been observed in the distance foraging on the pupal grounds, but we have, as yet, no definite proof that they feed on *Tyria*.

B. Pegohylemyia seneciella *Meade*.

(i) *Synonymy and distinctive characters.*

During the course of the weed-control investigations, a large number of Anthomyiid flies were bred from the capitula of ragwort from various areas in England and Scotland. They were kindly determined by J. E. Collin, a specialist in the group, as being chiefly *Pegohylemyia seneciella* Meade, with a few specimens of *P. jacobaeae* Hardy. *Chortophila* and *Phorbia* are synonyms of *Pegohylemyia*. The females of *P. seneciella* and *P. jacobaeae* are very similar, but Collin has found differences in the tibial bristles and the arista; they can be distinguished as follows:

	P. seneciella	*P. jacobaeae*
1.	No preapical bristles on hind tibiae	Three strong preapical bristles on hind tibiae, just above tarsus
2.	Arista not so pubescent as in *jacobaeae*	Arista more pubescent than in *seneciella*
3.	General colour usually dull grey	General colour usually more golden grey

Characters 1 and 2 also apply to the males, but these can easily be separated by colour differences, *seneciella* being much darker (almost black) than *jacobaeae* (grey-black).

The genitalia also differ, but as Mr Collin has prepared a paper, to be published shortly, dealing fully with the systematics and differences of these two species, I do not intend to deal further with them.

(ii) *Life history.*

The fly begins to make its appearance during the last week in June, coincident with the time when ragwort capitula are beginning to expand, and from the end of June onwards it is fairly common.

The eggs are laid both in the expanded and closed capitula, well down between the bases of the florets, usually one per capitulum, though very occasionally two eggs may be found in the same capitulum. The egg is white in colour, smooth, and glistening, oval in shape and tapering towards both ends. Its length is 0·84 mm., its breadth, at the middle, 0·28 mm. The incubation period is short, hatching taking place 3 or 4 days after oviposition.

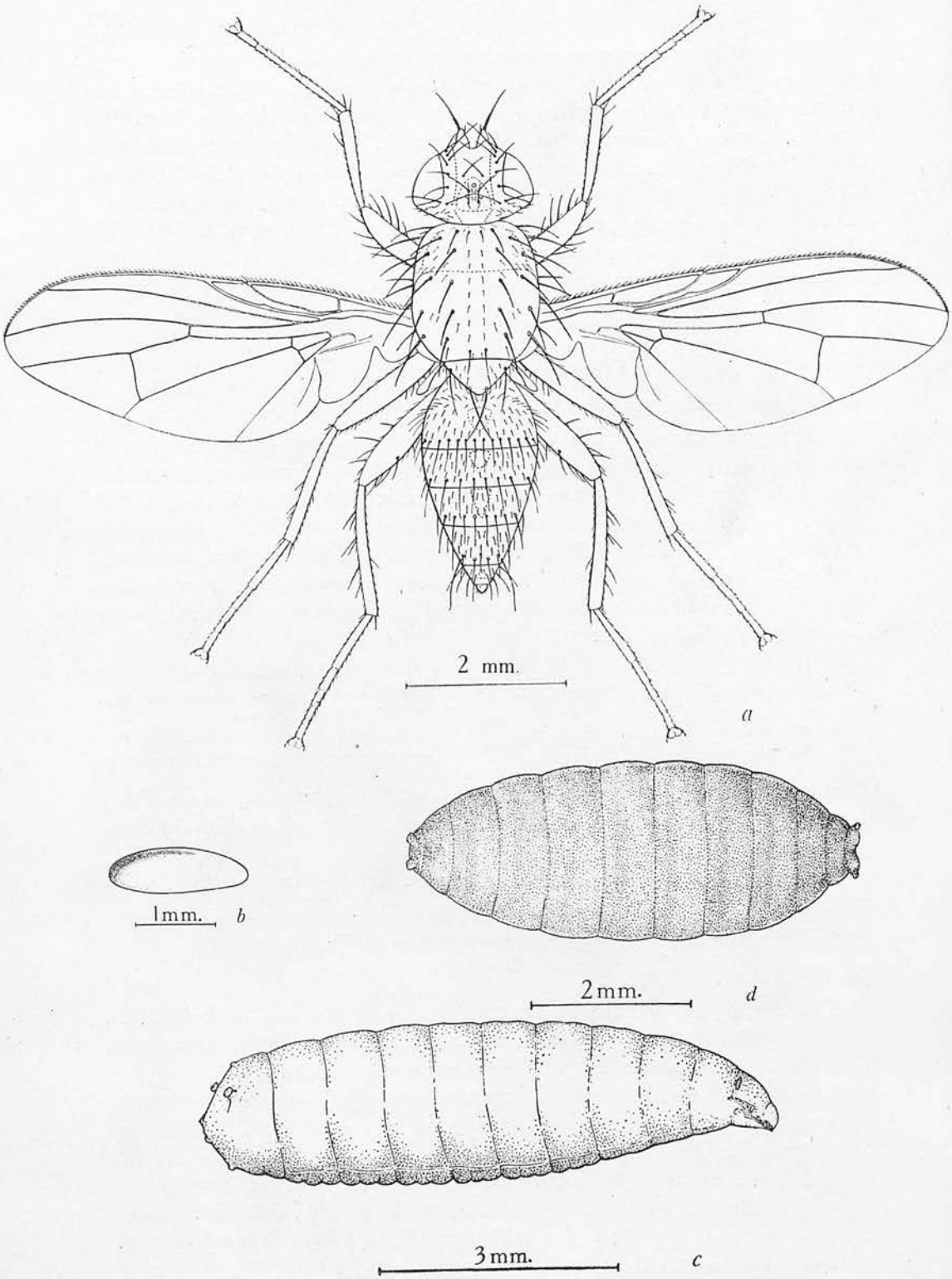

FIG. 8. *a*, *Pegohylemyia seneciella* Meade; *b*, egg; *c*, mature larva; *d*, puparium.

There are three larval instars, maturity being reached towards the end of August in the south, and later further north. In Ross-shire, Scotland, it is as late as the end of September. On maturity the larvae drop from the flowers and pupate in the soil. Mature larvae measure 7 mm. in length, puparia 5·5 mm.

Ragwort capitula infested with the larvae of *Pegohylemyia* are easily detected, on account of the dark brown central spot which characterises them. This diagnostic spot grows larger with the larvae, and is due to two causes: the withering of the florets in the region of the larva's activities, and the dirty colour of the matted florets, which the larva forms round itself as a kind of protective tube. This matting is probably helped by the extraction of a kind of cement from the tissues of the plant.

The larva eats the immature seeds, and part of the base of the involucre towards which end of the flower its head is directed. The percentage of infestation of, and the amount of damage caused by this insect, is discussed under the section dealing with the survey of insect damage.

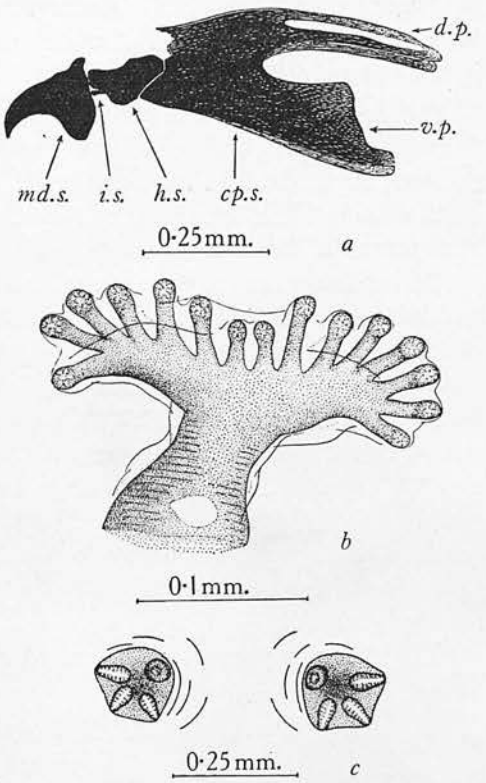

FIG. 9. *Pegohylemyia seneciella* Meade: *a*, buccal pharyngeal apparatus of mature larva; *b*, anterior spiracles of mature larva; *c*, posterior spiracles of mature larva. *md.s.* mandibular sclerite, *i.s.* interstitial sclerite, *h.s.* hypostomal sclerite, *cp.s.* cephalo-pharyngeal sclerite, *d.p.* dorsal process of cephalo-pharyngeal sclerite, *v.p.* ventral process of cephalo-pharyngeal sclerite.

(iii) *Parasites.*

A large number of larvae of *P. seneciella*, collected in the Farnham Royal area, were dissected for parasites. A solitary Braconid larva was found in 51 per cent. of the maggots. This parasite was later reared and identified as *Phaenocarpa ruficeps* Nees.

The following parasites were reared from the puparia:

Braconidae:	*Phaenocarpa ruficeps* Nees.
Ichneumonidae:	
Cryptinae:	*Hemiteles fulvipes* Grav. (hyper.)
Chalcidoidea:	
Pteromalidae:	*Lamprotatus splendens* Westw.
	L. obscurus Walk.

(*d*) *Biology of other ragwort insects.*

During the course of the investigations, several insects were observed to be causing damage to ragwort, but not in sufficient number to be of significance in the control of the plant. A few brief notes on these are included here:

(1) *Agromyza aeneiventris* Fln. This Agromyzid fly bores in ragwort stems, tunnelling the pith and reducing a great deal of it to frass. It also appears to do some slight damage to the adjacent layers of parenchyma. The imago, a small shining black fly, is a very common and pretty insect on ragwort from June onwards. Both larval and pupal stages are passed in the pith of the stem.

An estimation of the percentage larval attack, and of the numbers of larvae per infested stem, was made at Wentworth, Surrey; Hambledon, Bucks; Henley, Oxon; and Dorney, Bucks. At Wentworth, 31 per cent. of the stems examined were found to be infested, the average number of larvae per stem being three. At Hambledon, a 41 per cent. infestation was recorded, with a similar larval average of three per stem. At Henley and Dorney the infestation was 100 per cent., while the average number per stem at Henley was nine, and at Dorney 5·3. From these figures it will be seen that the fly is quite common on ragwort, but owing to the fact that its attack is confined chiefly to a non-vital part of the plant, the pith, its value as a controlling agent is relatively small.

The following parasites were reared from the puparia:

Chalcidoidea:	
Pteromalidae:	*Sphegigaster aculeatus* Wlk.
	Syntomopus thoracicus Wlk.
Cleonymidae:	*Caudonia agylla* Walk.
Cynipoidea:	
Eucoelini:	*Diglyphosema conjungens* Kieff.

Parasitism by the Cynipid, *Diglyphosema conjungens* Kieff., which has previously been recorded only from France, thus making the genus new for Britain, reached 15–17 per cent.

Other parasites of this fly recorded in the literature are as follows:

Braconidae:	*Dacnusa rufipes* Nees, from Europe.
	D. senilis Nees, from France.
	Gyrocampa senilis Nees, from Germany.
Ichneumonidae:	*Phygadeuon rusticellae* Bridg., from Germany.

Carduus nutans L., *Cirsium lanceolatum* L. (Scop.), and *C. eriophorum* L. (Scop.), are also recorded as hosts of *Agromyza aeneiventris* Fln.

(2) *Homeosoma* (*stem-borer*). A number of ragwort stems was kindly sent to me on September 15th, 1930, by Dr A. S. Watt of Cambridge, who collected them on the sand-dunes at Dornoch, Sutherlandshire. On examination they were found to be infested with a stem-boring lepidopterous larva. The collar

of the root was also observed to be attacked. Out of twenty single-stemmed plants, fourteen were found to be infested, thirty larvae in all being recovered, thus giving an average of two larvae per stem, and an infestation of 70 per cent. The plants were rather inferior specimens, such as one would expect from a sand-dune area, and appeared to have suffered rather badly as a result of boring attack. According to Dr Watt, the ragwort over a large area of the dunes seemed to be dying as a result of the infestation by this insect.

A single specimen was bred through and identified as *Homeosoma nimbella* Dup., a moth of the family Phycitidae. The following parasites were also reared:

Ichneumonidae:
Pimplinae: *Glypta rufata* Bridg.
Pimpla inquisitor Scop.

Two other species of *Homeosoma* are known to occur on ragwort in Britain—*H. cretacella* Rossl. and *H. nebulella* Hubn.

In New Zealand another species is already active—*Homeosoma vagella* Zell. The infestation of this moth in certain areas is reported to be as high as 80–90 per cent., and in others 100 per cent. It does not appear to have any controlling effect on vigorous plants, but in one area an important result of its activities was noted. On a farm were two paddocks, a few hundred yards apart, both containing ragwort which had been cut down once. In one, the infestation by *vagella* equalled 100 per cent., and in the other only 40 per cent. Where the borer had been particularly active in the 100 per cent. paddock, no secondary growth took place, whereas in the 40 per cent. paddock secondary growth was vigorous. The absence of secondary growth in the former was attributed to the effect of *vagella* on the crown of the roots, which were found to be largely rotted. If this insect is widespread, and an effective check to secondary growth, it should prove an important ally and auxiliary of *Tyria* in the control of ragwort.

It is, however, evident that, since New Zealand has already a lepidopterous stem-borer of the genus *Homeosoma*, there can be no further need for investigations on the allied British species, especially as the amount of damage caused by the British species does not seem to be greater than, if as great as, that already occasioned by *H. vagella*.

(3) *Leaf-mining Diptera.* Two species of leaf-mining Diptera have been recorded from ragwort—*Phytomyza albiceps* Fln., and *P. geniculata* Macq., both belonging to the family Agromyzidae. The common species observed and reared from ragwort in the South Bucks area is *Phytomyza atricornis* Mg. This species makes a narrow linear mine about 1 mm. wide, extending generally over the upper surface of the leaf. The egg, which is whitish grey in colour, and twice as long as broad (breadth 0·33 mm.), is laid in the leaf. The larva emerges in about 3 or 4 days. At Farnham Royal an average of three larvae per leaf was obtained. When fully fed it pupates generally on the under surface

of the leaf, just underneath the lower epidermis. Several generations occur in a year.

From the puparia the following parasites were reared:

Chalcidoidea:
Eulophidae: *Chrysocharis syma* Walk.
Braconidae: *Dacnusa areolaris* Nees.

Three further parasites are recorded in the literature:

Eulophidae: *Chrysocharis elongatus* Thoms. and *Solenotus viridis* Forst., both from Serbia.
Braconidae: *Paxilomma buccata* Breb., from Europe.

Another species which makes very much larger, irregular, blotchy mines is the Trypetid, *Spilographa zoe* Loew. The Chalcid parasite, *Lamprotatus obscurus* Walk. (Pteromalidae), has been reared from the puparia of this fly.

(4) *Sphenella marginata* Fln. This Trypetid fly was reared from a quantity of flower-heads collected in Norfolk, to obtain the emergence of mature *Pegohylemyia* larvae.

(5) *Aphis jacobaeae* Schr. This aphid is very occasionally found in clusters round the upper part of the stem of ragwort.

(*e*) *Survey of insect damage, with notes on plant reaction to attack.*

(i) *Method of study.*

Senecio jacobaea L., is a common weed throughout Britain. The two insects proposed for its control, *Tyria jacobaeae* L. and *Pegohylemyia seneciella* Meade, are distributed as follows: *Tyria* has a range extending from the south coast of England to the Caledonian Canal in Scotland. It is very plentiful in the south, in ragwort-infested country, but is scarce north of the Clyde. *Pegohylemyia*, on the other hand, is fairly well distributed throughout the country, from north to south, large collections having been made in Ross-shire, Scotland, not far from the northern seaboard. In some regions, however, its distribution is rather local.

A special study of the damage caused to ragwort by these insects was made in several areas in Buckinghamshire, Norfolk, Oxfordshire, and Surrey, England, while further notes were made on the activities of *Pegohylemyia* in the counties of Aberdeen and Ross, Scotland.

Some of these areas, having a fairly high infestation of ragwort, and being more or less removed from the routine of cultivation, which would have broken the natural sequence of events, as well as from interference from members of the public, were studied as "Type Areas". The populations of type areas were ascertained by means of a collapsible wooden square, each side of which measured 4 ft., giving a total area of 16 sq. ft. In taking the census several transects, 4 ft. wide, were made across the area in different directions. From figures obtained in this way, the population of ragwort plants per acre

was calculated. For seedlings, because of the difficulty of accurately counting the tiny plants, a smaller square, with 2 ft. sides, was employed.

A census similar to this was made of all the type areas. In following up the course of ragwort control by insects and other factors from year to year, a table of the following kind (with modifications to suit each area), providing, as it does, all the necessary data for quick and accurate comparison of different types of infestation in the field, is invaluable.

Area: Fawley Court Hill, Henley-on-Thames, Oxon, England. (Approximately 12 acres.)

Date of original survey: July 6th, 1931.

Type: Deer Park, overgrazed; occasional oak trees.

Soil: poor.

Altitude: 35 ft.

Association: chiefly grasses; permanent meadow.

Distribution: regular.

Mature plants per square yard: 22.

Mature plants per acre: 108,900.

Seedlings per acre: 152,460.

Plant type: Average height: 2 ft.
Range: 10 in., 1 ft., 2 ft., 3 ft. 8 in.
Average number of stems per plant: 1.
Average number of capitula per stem: 68.
Average number of seeds per capitulum: 70.
Average number of seeds per plant: 4760.
Larvae of *Tyria jacobaeae*: 1,216,800 per acre; 11 per plant.
Pegohylemyia: nil.
Other insects: *Agromyza aeneiventris* Fln. (stem-borer), common. *Aphis jacobaeae*: very occasional.

(ii) *Nature of* Tyria *attack and reaction of ragwort.*

The larvae of the cinnabar devour leaves, flowers, and part of the stems of ragwort. When the attack is really severe, as it nearly always is, an area of ragwort in full flower, such as the one we have just described, with 108,900 plants per acre, and 1,306,800 for the whole area of 12 acres, may be reduced to bare stems. Such reduction actually occurred in the two seasons of 1930 and 1931. A good idea of the havoc which is wrought by *Tyria* can be gathered from the illustration (Pl. XXI, phot. 2).

Superficial observation of a ragwort area after the deadly attack of the cinnabar, would naturally lead one to the conclusion that complete suppression and extinction of the weed must necessarily follow this entire destruction of leaves and seeds. Not so! Ragwort is possessed of recuperative powers, which can, and do, partly negative this result.

The reaction of the ragwort takes the form of secondary growth. When

healthy, vigorous plants are cut down in the early flowering stage, a number react by sending forth new shoots from the old stem. These ultimately produce a new crop of flowers, which later give rise to seeds. Failing this production, the crown of the root may become active, and begin to send forth small shoots, which, in the following spring, after the old stem has decayed, grow out to form a new plant. If the season is unfavourable, very little of either type of secondary growth takes place. It is a fairly general rule, however, in a good season, for attacked plants to make a second attempt at reproduction in one or both of the ways just described (Pl. XXI, phot. 3).

In addition to the observations made on the form and amount of this growth, following on *Tyria* attack, a number of experiments on the effect of wholesale and progressive cutting of ragwort, designed to simulate insect attack, were carried out. From these experiments, results comparable with those following true insect damage were obtained.

The first experiment in this direction was carried out at Wentworth, Surrey, on fairly good land left derelict for future building purposes. Ragwort was present on this area to the extent of 40,000 plants per acre. On July 3rd, 1930, several acres of these plants, having an average height of 4 ft. 1 in., and an approximate seed number of 115,240, were mowed down to within 2–4 in. of the ground. Nearly 4 months later (October 31st, 1930), the field was again a mass of ragwort flowers, except for a control area of several hundred square yards, where a large number of uncut plants had attained maturity and seeded, during the first fortnight of September, about six weeks previously. These control plants were now dried up and withered, whereas the new shoots and flowers produced secondarily from the bases of the cut plants were still fresh.

A comparison of seed yields, height, and time of flowering, of the attacked and unattacked plants follows:

	Uncut plants	New growth of cut plants
Height	4 ft. 1 in.	2 ft.
Number of stems	10	15
Capitula per stem	179	40
Seed yield	115,240	39,945

The seeds of the uncut plants ripened during the first fortnight in September, while those from the secondary growth of the cut plants did not attain maturity until the end of November. From this experiment, carried out over an area of 5 acres, the following conclusions were drawn.

The cutting of strong healthy specimens of ragwort to within 4 in. of the ground, shortly after the flowers have opened (when *Tyria* attack is commencing) results in:

(1) The production of secondary shoots which produce flowers, and ultimately seeds.

(2) An increase of 50 per cent. in the number of stems, the average thickness of the new stems being half that of the old.

Phot. 2. Illustrating the effect of *Tyria* larvae on Ragwort. Left—normal Ragwort plant; right—plant entirely denuded by caterpillars.

Phot. 3. Illustrating plant reaction to attack. Left—flowering Ragwort plant; right above—cut to within 4 inches of ground; right below—secondary growth from base of cut stem.

(3) A secondary seed yield equal to 34·7 per cent. of the yield potentially producible, in the absence of attack.

(4) A retardation of seed ripening by 10 weeks.

The next experiment consisted in the progressive cutting of transplanted ragwort in the Laboratory garden. From one lot all the leaves were removed, from another all the capitula, and from the remainder, all leaves, flowers, and top portions of the stem. In interpreting the results of this experiment, the condition of the plants must be considered. They had been transplanted in the late rosette stage and as a result had used up some of their reserves in becoming established, so they are equivalent to plants which are none too vigorous, growing on poor soil, with little reserve food to draw on in case of emergency.

The lot having all leaves removed produced a number of small new leaves. The seed yield was reduced by 10 per cent. Those with all the flowers nipped out produced a new lot of capitula. The seed yield was reduced by 60 per cent. In the remaining lot, where leaves, flowers, and the top part of the stem were cut off, no reaction took place and the plants died.

From this series of experiments on wholesale and progressive cutting of ragwort, we may draw the following main conclusions, which were confirmed by further observations in the field:

(1) A badly attacked plant, if originally vigorous and if the growing season is good, has enough reserve energy to produce a second crop of seeds equal to 34·7 per cent. of the original potential yield producible in the absence of attack, thus reducing a total loss of 100 per cent. to one of 65·3 per cent.

(2) Plants with little or no reserve energy, growing on very poor soil, when badly attacked, do not produce seeds secondarily.

(3) Many plants which are not able to produce a second crop of flowers and seeds in the year of attack may send out small shoots from the base of the stem. These shoots grow vigorously in the following year, and are often capable of producing more seed than the original plant. Field observations show that this method of secondary growth has the effect of prolonging the life of the plant beyond the ordinary biennial period.

(4) Damage to any part of the plant, leaves, stem, and flowers, will lower the seed yield for that season.

Passing on to the consideration of actual attack by *Tyria jacobaeae*, we find these results verified.

At Henley-on-Thames, ragwort, infesting 12 acres of deer-pastured meadow, was found to be heavily attacked by *Tyria*. On July 11th, 1930, all the plants had been eaten leaving bare stems. On September 12th, 1930, when the area was re-visited, numerous secondarily produced flowers were observed, the field being a mass of yellow flowers. Calculations revealed that the seed yield from this secondary flower growth was equal roughly to 35–40 per cent. of the potential seed yield, a result similar to that of the large-scale cutting

experiment at Wentworth. This same area in 1931, after similar heavy *Tyria* attack, had only an occasional plant reproducing secondarily. Such a condition can be accounted for by the unfavourable season, and the consequent reduction of reserve food supplies.

At Wentworth A area, Surrey, an area with medium sized, not very vigorous plants was kept under observation. A plot, 16 sq. ft. in area, was mapped out, and the following notes made:

July 3rd, 1930. Number of plants: 14.
Average height: 2 ft.
Average number of *Tyria* larvae per plant: 15.
Approximate total number of larvae: 210.
Estimated seed yield per plant: 20,000.
Estimated seed yield for area: 280,000.

On September 12th, 1930, all fourteen plants were eaten to bare stems by *Tyria* larvae and eight showed initial secondary growth, with a new seed production of (1) 4020, (2) 2680, (3) 938, (4) 804, (5) 2010, (6) 1675, (7) 670, (8) 835; i.e. a total of 13,632 seeds. The estimated seed yield in the absence of attack was 280,000 seeds, while the actual yield produced secondarily was 13,632 seeds. This means a conversion of a 100 per cent. loss to a 95 per cent. loss.

Another similar plot had a secondary seed production of 12,199, and an estimated seed yield of 270,000, again a conversion of a 100 per cent. loss to one of 95 per cent. In this area the plants were of poor quality, and lacking in reserves, hence the drop in secondary yield as compared with the Henley area.

Another plot at Littleworth gave results similar to Wentworth A area. This plot had an area of 1296 sq. ft., with thirty-six plants, averaging 2 ft. 3 in. in height. The estimated potential seed yield was 381,900. After a heavy attack by *Tyria* secondary growth produced 19,263 seeds. This is equal to 6 per cent. of the potential seed yield, or a 94 per cent. loss.

An even more impoverished area with poorer plants was observed at Stoke Poges:

Size of area	136 square yards
Number of plants	14
Height	2 ft. 6 in. to 3 ft.
Estimated seed yield for area ...	331,650

On July 29th, 1930, all fourteen plants were reduced to bare stems by *Tyria*. Observations were made up to November 20th, 1930, but no secondary growth occurred. Therefore seed loss was equal to 100 per cent. Reserve food in this area, either in the plant or in the soil, was reduced to a minimum, so that the infestation was wiped out.

These various experiments on the reaction of ragwort to cutting, and to insect attack, clearly illustrate one important way in which the biological control of noxious weeds differs from the biological control of noxious insects.

In the case of the insect pest, the damage produced by a single parasite is normally sufficient to destroy its host. In the case of a plant pest like ragwort we have to reckon with a reactive power for reproduction, which partly nullifies the destructive effectiveness of the natural enemy feeding on it. This reactive power is absent in the insect. Its absence, coupled with the greater ease with which an insect can be killed, accounts for the greater success in insect control work.

(iii) *Effectiveness of* Tyria *as a control.*

From superficial observation of the tremendous havoc which *Tyria* causes amongst ragwort infestations, one might come to regard this moth as an ideal control, were it not for the fact that in many of these devastated ragwort localities the infestation often proves to be as high in the year following the attack. This is due, as we have already seen, largely to secondary growth. On the other hand, secondary growth does not always occur. It does not occur in an unfavourable season even in fairly vigorous plants, and it rarely occurs, even in a good season, in inferior plants growing on poor and ungenerous soils. Under these two sets of conditions, *Tyria* is an effective control.

The area at Fawley Court Hill, Henley, will illustrate the effectiveness of control when secondary growth, owing to the unfavourable season, was eliminated.

On June 21st, 1932, this extensive type area of 12 acres, which in 1931 had a population of 108,900 mature plants per acre, or 1,306,800 for the whole area, and 152,460 rosettes per acre, or 1,529,520 for the whole area, was observed to be entirely free from mature ragwort, except for about a dozen scraggy plants, 6 in. high, at one corner. Young plants were also absent from the whole area, except for one or two odd specimens. In 1931, *Tyria* attack on this area was considerable, there being approximately 15,681,000 larvae on the area, or an average of twelve per plant. Owing to the unfavourable season of 1931, no secondary growth took place, and, consequently, there was no seed to produce seedlings in 1932[1]. Those actually occurring must have arisen from a few odd seeds which escaped the ravages of *Tyria*. The wholesale clearance in 1931 of the ragwort leaves, seeds, and top parts of the stems, coupled with the absence of secondary growth, resulted in the apparently very satisfactory control.

On the day the field was visited (June 21st, 1932), a large number of *Tyria* moths was seen flying about, seeking in vain for plants on which to oviposit.

The natural sequence of events in this area appears to be that *Tyria*, owing to the absence of food plants, will very largely die out. To prevent reseeding of the area from the outside, certain precautions, which will be dealt with

[1] In 1930 the attack of *Tyria* on this area was tremendous, equal in intensity to that of 1931; nevertheless, the area maintained, in 1931, a population of over 100,000 plants per acre, similar to that of 1930. This population was produced (in the favourable season) from a secondary crop of seeds, and from secondary growth at the base.

later, must be taken. Effective control was also brought about by *Tyria* at Stoke Poges, where a small infestation of ragwort, growing on very poor soil, was exterminated.

After observations over a wide area, the following conclusions have been drawn regarding the effectiveness of *Tyria* as a control:

(1) Provided that the attack is general (see "Types of Land" (3), p. 309) and that no secondary growth follows, either in the shape of a new crop of flowers, or of new growth from the base, to carry the ragwort over into another year, *Tyria* can be a very effective controlling agent.

(2) When poor plants, growing on very inferior soil, are heavily and uniformly attacked by *Tyria*, the ragwort infestation should be wiped out.

(3) Once an infestation is under control, certain precautions have to be taken in order that the area may be kept free of ragwort. These take the form of (*a*) stimulation of grasses in the area, (*b*) avoidance of overgrazing, etc., and are discussed in a later section.

(iv) *Effectiveness of* Pegohylemyia *as a control.*

Pegohylemyia is an internal capitulum feeder. The eggs are laid amongst the flowers in the expanded and half-opened stage, usually one per capitulum. On emergence the larva commences to eat the seeds. The infested florets are easily recognised by a brown spot in the disc, which grows larger as time goes on. This is due to the premature withering of the central flosculi. As the larva feeds, it mats some of the florets around it, probably as a protection from parasites. Sometimes it pierces through the receptacle into the stalk.

In order to ascertain the extent of the infestation of this fly, and the amount of damage which it causes, ragwort flower heads were examined from various areas throughout Britain, among which may be mentioned Stanford, Norfolk and Medmenham, Bucks, in England; and Banchory, Aberdeen, and Achterneed, Ross-shire, in Scotland.

Material examined at Banchory, Aberdeen, on August 30th, 1930, was found to have 21·8 per cent. of the capitula infested with the larvae of *Pegohylemyia*. 70–75 per cent. of the seeds of each infested capitulum had been destroyed.

At Stanford, Norfolk, the infestation per 100 capitula was only 8·7; at Medmenham, Bucks, 8·5; while at Achterneed, Ross-shire, Scotland, the peak figure of 33·7 was reached. The percentage of seeds eaten by each larva was about 70–75 per cent. of each capitulum, a capitulum averaging roughly seventy seeds.

The position of *Pegohylemyia* as a control is as follows: in Southern England it infests approximately eight to nine of every 100 capitula, and in the capitulum attacked, 75 per cent. of the seed is destroyed. In Northern Scotland its capacity as a destructive agent to the seed output appears to be much greater, for it attacks approximately thirty-three or thirty-four out of

every 100 capitula. The northern range of this insect, so far as larger numbers are concerned, is much greater than that of *Tyria*, which does not extend much further north than the south of Scotland (found sparsely as far north as the Caledonian Canal), so that *Pegohylemyia* has the advantage of 200 miles, or even more to the northern limit. This advantage may perhaps be useful in New Zealand in higher and colder regions, where it may be impossible to establish *Tyria*.

(v) *General survey of ragwort control in Britain.*

A brief description of the main types of ragwort infestations in this country, where some degree of control has been effected, will indicate how the work should progress at the other end.

In Britain three main types of land have been observed in connection with ragwort control by insects:

(1) Good farm land. Ragwort is controlled on this type of land by proper cultivation, coupled with the maintenance of a good turf and the avoidance of overgrazing.

(2) Poorer land, with ragwort in comparatively small areas, isolated from extensive ragwort country. As we have already seen (pp. 306, 307), ragwort infestations have been controlled in areas of this type by *Tyria*. Once control is attained in such areas, the problem is to effect its continuance. If a field is isolated from other ragwort by woods and good farm land, a lot of seed should not find its way in from outside. However, in order to forestall the fulfilment of such a possibility, the pasture grasses must be given a chance to come away strongly, so that they may form a soil covering, sufficiently dense to preclude the re-establishment of ragwort seedlings. This could be effected in three ways: firstly, by the prevention of grazing for a period; secondly, by stimulation of the grasses present with artificial manures, such as lime and basic slag, etc.; and, thirdly, by killing rabbits and other animals which expose the soil surface, thereby providing ragwort with a suitable seed bed.

In some areas, such as part of Stoke Poges already referred to, the land is so extremely poor and hard that the plants never acquire sufficient vigour to reproduce themselves secondarily: consequently *Tyria* attack is very effective. Owing to the infertility of the soil, it is not possible to maintain a close uniform cover of grass, so the measures proposed in the preceding case are inapplicable or unnecessary. When present, *Tyria* ought to be quite effective by itself on land of this sort.

(3) Extensive ragwort country, many square miles in area, where the soil is poor and much of the surface exposed by direct and indirect rabbit activity, provides ideal conditions for the establishment of ragwort seedlings. Much of the Breckland of East Anglia, which in addition to rabbit-exposed soil has large areas of derelict arable land, too unproductive to reward further cultivation, is of this type. Several factors militate against the achievement of

control by *Tyria* in this desolate country. *Tyria*, although widespread, is only locally abundant. Consequently, when small areas, with badly attacked ragwort showing no signs of secondary growth, are brought under control, as at Henley, they become supplied with new seed from the unattacked ragwort, which has a plentiful supply for dispersal. In this manner the ragwort is maintained in the area.

The real stabilising factor of the infestation, however, is rabbit activity, which has caused a break in the plant community, with consequent exposure of the soil surface. If rabbits were to be excluded from this region, the natural succession of plants which occupied the derelict areas prior to cultivation would gradually cover the soil and effectively prevent the establishment of ragwort seedlings, so that the infestation would come to an end. This has already taken place in certain areas of Breckland.

Therefore, to anyone attempting to control this weed, we cannot too strongly emphasise the importance of eliminating factors (such as rabbit activity, and overgrazing by farm animals), which predispose to open soil conditions.

One way of dealing with a poor unproductive area like Breckland would be to lay it down to forest. Several large portions have already been planted by the Forestry Commission with Scots pine, etc., not for the purpose of controlling ragwort, although it has done this very effectively, but in order to make use of waste land, and to build up a reserve of timber for the future.

VI. THE ECOLOGY AND CONTROL OF RAGWORT IN NEW ZEALAND.

(1) Biological control.

The control of ragwort in England has been discussed in Part v. In New Zealand conditions are somewhat different. The Dominion is essentially a grazing country, and cultivation occupies a minor place in the work of the farmer. On the better class farms, where the land is good, ragwort is kept under control as it is under similar conditions in Britain. It is on the poorer types of pasture land, and on the large areas of bush grasslands, where cultivation has never taken place, that ragwort is a menace. Possibly two other factors, in addition to the absence of the insect fauna, enter into the explanation of the ragwort problem of New Zealand. These are the poor quality of the soil, especially in the North Island, which has had to import many millions of tons of phosphates to improve it, and the unorthodox method of pasture production (i.e. sowing on burnt-over areas which have not been ploughed) with the establishment of poor strains of grasses and clover.

A complex of four main insects will be concerned in the efforts to effect some sort of control of the ragwort pest. These are:

Tyria jacobaeae L. (introduced): seed- and leaf-eater.
Nyctemera annulata Boisd. (native): as *Tyria*.
Pegohylemyia seneciella Meade (introduced): seed-eater.
Homeosoma vagella Zell. (native): stem- and crown-borer.

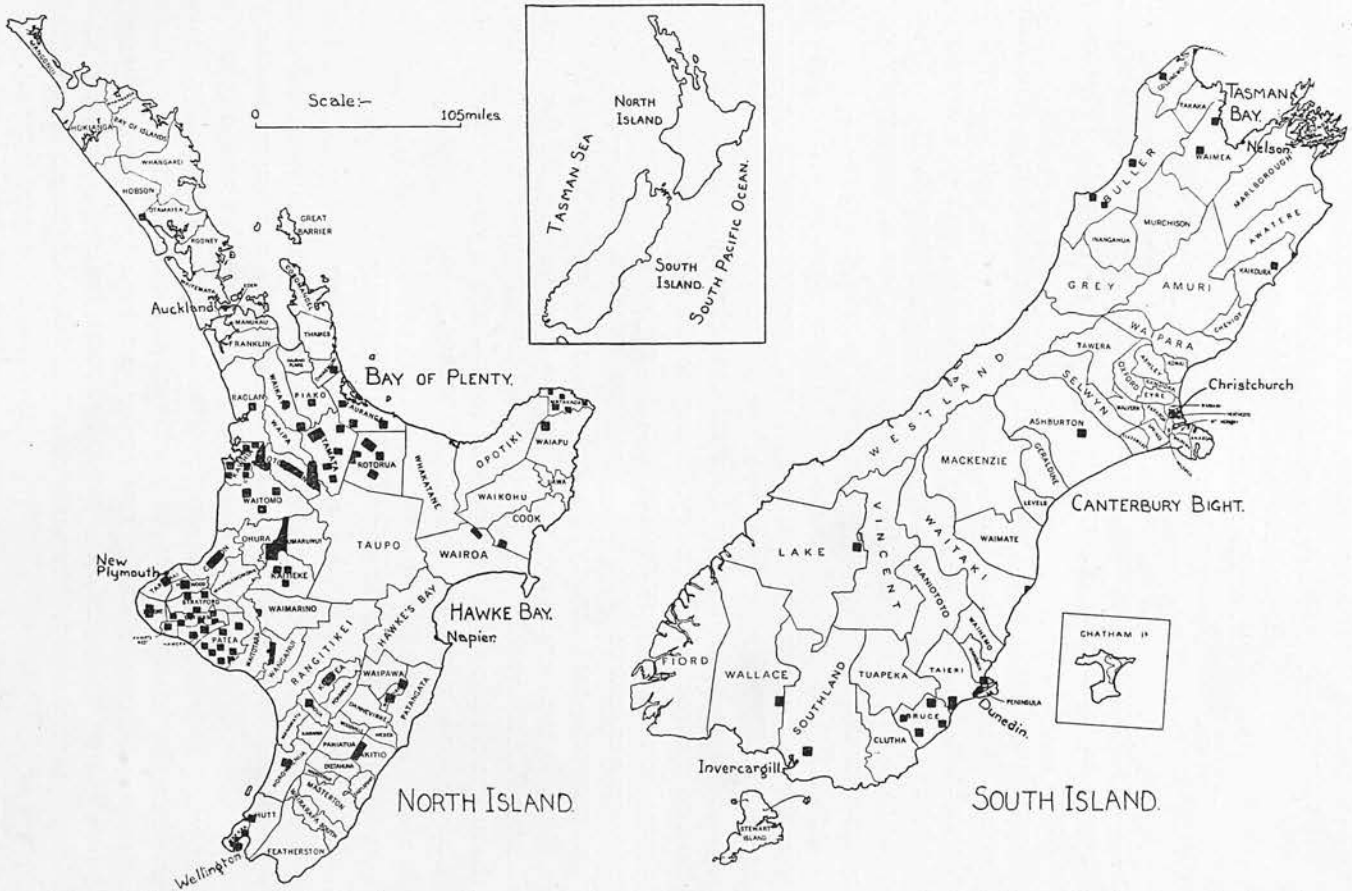

FIG. 10. Map showing main distribution of ragwort in New Zealand. (Survey carried out by Dr Miller of the Cawthron Institute.)

In New Zealand the following native insects are recorded from ragwort:

Lepidoptera.	*Nyctemera annulata*: attacks leaves and flowers.
	Homeosoma faranaria: stem-borer.
	H. vagella: stem-borer.
Diptera.	*Agromyza* sp.: pith-borer.
	Phytomyza affinis: leaf-miner.

The Lepidopteron, *Nyctemera annulata* is attacked by the Ichneumonid, *Echthromorpha intricatoria* F., and by the Tachinid, *Lydella* (*Phorocera*) *casta* Rond.

Tyria, *Pegohylemyia*, and *Nyctemera* will deal with the seeds as effectively as they can. When secondary growth follows in their train their work will be partly nullified. This may be partly obviated by the work of *Homeosoma*, boring in the crown of the roots and preventing any new growth. If conditions turn out to be similar to those of the Henley area, where no new growth took place in an unfavourable season, progress will be quicker and easier.

Whether *Tyria* and *Pegohylemyia* will be more effective in New Zealand than in Europe it is impossible to say. It was hoped at one time that in the warm New Zealand climate *Tyria* would pass through two generations in a season and thus increase greatly in destructiveness; but up to the present there has been no change in its life history. It may be also that *Tyria* will suffer less from parasitic attack in New Zealand than in Europe (though two parasites of a very common native Noctuid, *Nyctemera annulata* Boisd.—which also feeds on ragwort—have already attacked it; one species, the Tachinid *Lydella casta* Rond. in the larval stage, the other, the Ichneumonid, *Echthromorpha intricatoria* F. in the pupal stage), but the possibility of ragwort being favoured by the milder climate and longer growing season, with a greater likelihood of secondary growth, might outweigh this advantage.

(2) Other methods of control.

(i) *Cultural methods.*

On the better class farms of Britain, ragwort is successfully controlled or prevented from obtaining a footing by good cultivation and the maintenance of good pastures. This may be described as the preventive method, and is undoubtedly the best one. In areas where the land is of poorer quality, or on farms where the management is not so efficient as it ought to be, or again on dairy pastures where the land is kept under grass for a long period of years, with overgrazing, the stimulation method of control may be employed. This consists in the treatment of the pastures with suitable fertilisers. A good turf is the result, and this will effectively prevent seedling establishment. The existing ragwort plants must, of course, be removed entirely, root and stem.

The experience of a Sussex farmer with this method may be cited. When he took over a farm of 300 acres, the grassland was heavily infested with

ragwort, "as thick as corn in some fields". During the first summer he mowed it down, but this process, according to neighbouring farmers, had not hitherto proved successful. In November, an application of 5–6 cwt. of basic slag to the acre was made and the grass harrowed. At the end of three years, 200 acres of the grassland had been slagged. Results in the summer following on the first application proved the method, on the worst land, to be a success. This farmer continued to dress his land with slag every other year, until at the end of 10 years ragwort was entirely eradicated, and the farm was able to support twice as much stock as it did prior to the application of fertilisers.

To accelerate the process, the mature ragwort plants, at the time of commencement of fertiliser application, and in the following year, should be entirely removed. This process is known as "stubbing". A sharpened hoe or a small spade with a keen edge is used as a stubber, and with either of these implements the entire plant is removed. A number of rootlets occasionally get left behind, and these, it is said by farmers, may produce new plants in the following year. A second round with the stubber will get rid of these and the fertiliser part of the method will effectively prevent the establishment of seedlings.

Another method of getting rid of the mature plants is to pull them up by hand, after rain has softened the soil. Still another method is to mow down the weed at certain periods of the year, when the plant is just coming into flower, and when the secondary growth has been fully formed. According to the experience of several farmers, this type of control is not very effective unless carried out over a period of years.

(ii) *Grazing.*

The importance of preventing overgrazing by stock, if ragwort is to be excluded from the composition of the pastures, has already been emphasised. For a comprehensive account of the management and care of pastures, the reader is referred to books like *Range and Pasture Management* (by A. W. Sampson—John Wiley and Sons, Inc., New York, 1923), etc. Davies in "Grazing" (*Bull. Bur. Pl. Genet.*, Aberyst., No. 10, 1933) gives the following advice for the maintenance of a good pasture: "Controlled intermittent grazing at all times of the year; the length of the rest period and the intensity of grazing to be determined by the pasture type concerned, and the demands of the species which it is desired to encourage."

The method of ragwort control by stocking infested pastures with sheep has long been known. It has proved very successful, but unless certain precautions are taken, a high mortality amongst the sheep may ensue. Cattle and horses will not eat ragwort unless forced to do so, but sheep are very fond of it, especially when it is in the young rosette stage. Although they are fairly tolerant to the poisonous principles of the weed, long-continued feeding on ragwort alone will ultimately prove fatal.

It is necessary, then, when this type of control is to be tried out on pastures heavily infested with ragwort, to divide the fields up into small areas, so that the weeds in each area are very closely eaten. The sheep must be transferred occasionally to weed-free pasture or else a high mortality will occur.

Old ewes are much less susceptible to ragwort poisoning than are the younger animals, hence they have been employed more successfully. As well as this greater degree of tolerance to the poison, they have an added advantage in that they attack the crown or growing region of the rosette, whereas the younger sheep eat the outer leaves. The attack on the crown is more quickly and more certainly effective.

Ragwort control by means of sheep should be carried out during the late winter and early spring, when the weed is in the rosette stage. It is then succulent and inviting, while the pasture is uninviting. At this stage too, the plant contains a smaller proportion of poisonous alkaloids. Sometimes sheep are allowed to feed continuously on ragwort when it is in full bloom. This procedure is invariably followed by fatal results. On dairy farms liable to a slight or moderate ragwort infestation, it is a good plan to allow a few old ewes to graze along with the cattle throughout the year. They will successfully keep the pasture free from ragwort.

(iii) *Application of chemicals.*

During the last few years various experiments have been carried out by the New Zealand Department of Agriculture, to test the effectiveness of the chlorates of sodium and calcium in weed control. Ragwort, because of its abundance and menace to dairy farmers was chosen for prior treatment. Both chlorates successfully killed the weed, but for various reasons sodium chlorate was found to be more suitable for use, and at the same time its killing properties were proved to be stronger than those of the calcium salt. On the other hand, sodium chlorate presents a risk of fire. When clothes which have become wet with the spray are dried, they ignite easily when placed near an open flame. A French preparation of the salt, "Occysol", obviates this fire risk, while, at the same time, its effectiveness in killing the weed is equal to 98 per cent. of that of the pure chlorate.

Sodium chlorate can be used for killing ragwort either in the dry crystalline state or in the form of a spray solution. The solution is preferable, one of 3–5 per cent. concentration giving a 100 per cent. kill. The plants should be sprayed during the winter and spring, when they are in the rosette stage; a 4–5 per cent. solution is then advisable. When the plants are entering the flowering stage a 2 per cent. solution is strong enough. Although the mature plant thus appears to be receiving a much smaller amount of chlorate, in reality it may be receiving more than the rosette, for it requires a much larger amount of the solution to wet it.

The spray does not affect grass, nor is it poisonous to stock. It does,

however, render the weeds more attractive to stock, who may eat them and suffer from ragwort poisoning. Care must be taken then, for a short period, to prevent the animals from gaining access to the sprayed weeds.

Another chemical preparation tested for ragwort control was a mixture of common salt, three parts, and iron sulphate, one part. This is applied in the dried state and is effective for small infestations.

VII. MASS COLLECTIONS AND SHIPMENTS OF WEED-CONTROLLING INSECTS.

During the course of the ragwort, gorse, and blackberry control investigations, the writer collected nearly three-quarters of a million insects for shipment to New Zealand. Out of this number, about half were intended for the control of ragwort.

The collection of suitable insects for shipment in large quantities is one of the major problems of a weed control project. A great deal of time, trouble, and money was spent on this branch of the work.

Tyria jacobaeae L. The chief collecting area for pupae of the cinnabar is situated in East Anglia, in the Breckland region of the county of Norfolk. The Breckland consists of huge areas of unproductive soil, strewn with small flints; in fact it is an area partially approaching the steppe type. At one time portions of this land had been enclosed from ancient commons, and ploughed or broken up (Breck = broken), hence the name Breckland. The ploughed areas ultimately proved unproductive and were largely allowed to return to their natural state. They are occupied in places by heather, bracken, and dwarf grass vegetation. Some of the Breck associations are made up of the grasses *Festuca ovina*, *Agrostis tenuis*, and *Aira praecox*; the mosses *Hypnum cupressiformae*, *H. schreberi*, *Hylocomium triquetrum*, *Leucobryum glaucum*; and other plants including *Galium verum*, *G. saxatile*, *Alchemilla arvensis*, *Rumex acetosella*, *Urtica dioica*, *Dactylis glomerata*, *Potentilla erecta*, *Sedum acre*, *Cerastium vulgatum*, *Cirsium* spp., etc. In certain areas of the wastes of the open dwarf grass association, large quantities of ragwort are found.

In addition to the permanent Breck, there are areas of agricultural land, which, owing to the poor returns for cultivation, have been left derelict by the farmers and are gradually reverting to the Breck type. Ragwort is usually abundant on such land.

The soil of the Breckland is light, chalky, and sandy, and receives an annual rainfall of 22·5 in., one of the lowest in England. Such a country offers an excellent opportunity for the establishment of ragwort, ultimately because of its soil and climate, and immediately because of the relative openness of the vegetation, and because of the greatly diminished plant competition. The openness of the vegetation is intensified by the burrowing of innumerable rabbits, which create additional suitable seed beds for the establishment of ragwort seedlings.

Headquarters for the collection of pupae were established at Stanford, a lonely hamlet in the wilds of Breckland. Work began about the end of July and continued throughout August. Collecting proved to be a slow business, until speeded up by the employment of local workers, chiefly women and boys, to whom payment was made at a given rate per thousand. The procedure involved in the collection was as follows. First of all, the country was explored by car, in order to locate suitable collecting grounds. Although the characteristic alternating yellow and black banded larvae were very numerous in many areas, suggesting an easy and plentiful supply of pupae, the finding of areas where the latter might be obtained in sufficient quantities to warrant the transportation of workers to them, was often very difficult. In some places where numerous small flints were scattered over the ground, the collection, though slow, was easier. These stones were turned over, and under the smaller, flatter types, pupae were often found in nests of 1, 2, 3, or 4, and occasionally 6 or 7. When supplies from this source were exhausted, resort was made to the grassy and mossy parts of the area. The grass and moss were pulled up in handfulls, and grubbing in the surface layer of the soil revealed the pupae.

The daily collections were brought back to headquarters, stored in appropriately ventilated boxes, with damp moss as packing, and conveyed periodically to the laboratory by car. On arrival at Farnham Royal, the pupae were sorted prior to shipment. All malformed and small specimens, also those of a dull black colour, which were usually parasitised or attacked by fungi, were discarded. Only healthy looking pupae of a bright reddish brown colour were selected for shipment. The pupae were finally packed in small tin boxes, with slightly damp sterilised sphagnum as packing material, the moss providing the requisite humidity. These tins were also packed with sterilised sphagnum, in larger wooden boxes, and were then ready for shipment.

Shipments were made from the Royal Albert Docks in the boats of the Shaw, Savill, and Albion Shipping Co., and the New Zealand Shipping Co., whose agents were very helpful in making arrangements for the conveyance of the insects in the vegetable chamber of the various vessels concerned. A fairly equable temperature of 34 to 38–40° F. was maintained in these rooms, so the pupae were unaffected by the greater variations of temperature experienced on the voyage. On arrival at Nelson, New Zealand, the shipments were met by an official of the Cawthron Institute, previously advised by cable, and the insects conveyed to the quarantine insectaries, there to await further testing and ultimate liberation.

An attempt was made to send eggs of *Tyria*, but none of these hatched after their arrival in New Zealand. In all, 294,382 *Tyria* pupae were exported to New Zealand.

Pegohylemyia seneciella Meade. Different methods of collection were employed for this insect. Owing to the smallness of the puparia, no attempt was made to collect in this stage, as the numbers so recoverable, after the

expenditure of a great deal of time and labour, would have been negligible. The material was collected in the late larval stage. The florets of ragwort infested by the larvae of *Pegohylemyia* were easily distinguished by the dark brown central spot on the disc, which became larger as the larvae grew older. The time for collection was determined by the size of the larvae. When they were considered to be nearly mature, the heads of the plants with a fairly high infestation, were collected *en masse*, and packed in sacks. At the end of the day the sacks were despatched by passenger train to the laboratory. In

FIG. 11. Consignment of ragwort control insects ready for export to New Zealand. Top centre box open to show packing method.

making these collections two main points had to be kept in mind: first the actual time for collection is very short, as the larvae, when mature, quickly drop to the ground for pupation and so are lost; and secondly, collection of the larvae before maturity is attained, will result in undersized puparia. Thus it will be seen that for a successful collection of *Pegohylemyia*, one must be on the alert for the critical stage. This insect was collected in Norfolk, North Lincolnshire, and Yorkshire, while a number were sent from Ross-shire in Northern Scotland.

On arrival at the laboratory, the flower-heads were spread out on trays in the insectaries. Daily collections of larvae and puparia were made from

the bottoms of the trays, and the final selection of puparia packed in tin boxes with slightly damp sphagnum moss, in the manner already described for *Tyria*. A total of 58,000 puparia of *Pegohylemyia* was shipped.

While the ragwort investigations were proceeding, shipments of gorse and blackberry insects were made from time to time.

Apion ulicis Forst. Shipments of this gorse-controlling beetle were made in the adult stage. At first they were collected by beating the gorse bushes and allowing the various insects to fall into nets held underneath. The Apions were then separated from the conglomerate mass of pods, thorns, and various insects, by means of sucking tubes.

Later, in order to maintain the absolute purity of the species, gorse pods, containing mature *Apion* larvae, were collected from the gorse bushes in August. These were spread out in cages in the insectary, where on reaching maturity, the weevils, being themselves unable to force a way out, were liberated when the pods burst, as a result of the drying action of the sun's rays. The beetles thus collected were placed in muslin bags, containing gorse twigs, which had their ends waxed to conserve moisture and freshness. A number of these bags were then placed in adequately ventilated wooden boxes for final shipment.

In all 273,260 individuals were shipped to New Zealand.

Coraebus rubi L. This Buprestid beetle, intended for the ultimate control of blackberry, was collected in the Antibes area of Southern France. The collection was carried out by a field agent in the *Coraebus*-infested rose nurseries of that region, where the insect is so injurious that many nurserymen are reported to be going out of business owing to its attacks. During the autumn and winter months the rose stocks containing larvae of *Coraebus* (identified by cutting a thin slice from the side and so revealing the brown galleries of the root-boring larva), were collected and sent in cane hampers covered with sacking, to Farnham Royal. At the laboratory they were examined and repacked tightly in wooden boxes, for export to New Zealand.

In all 7647 infested rose stocks were shipped, thus bringing the grand total of selected insects for export to 633,289.

SUMMARY.

1. Ragwort (*Senecio jacobaea* L.) was introduced into New Zealand from Europe prior to 1874, since when it has become a very serious pest in the Dominion. Its wide and rapid spread was attributed to the absence of the European insect fauna, which exercised a controlling effect on the weed in its native lands. Accordingly, the present investigation was undertaken in order to discover the factors, insect or otherwise, which kept ragwort under control in Britain, with a view to their ultimate utilisation in suppressing the pest in New Zealand.

2. The paper opens with an account of the initiation of the New Zealand Noxious Weed Control Scheme, and a summary of previous attempts to subjugate weeds by the biological method.

3. The main principles underlying the biological control of weeds are summarised and the procedure to be followed in work of this kind indicated. One of the dangers in weed control by insects is the possibility that the introduced species may migrate from the weed to plants of economic value. With proper safeguards this risk is greatly minimised. Several experiments dealing with this problem are quoted, and the subject discussed.

4. Ragwort is described in its various stages, while details of the life history of the weed, the history of its introduction into New Zealand, its botanical status, relation to plants of economic value, its poisonous properties, together with the diseases which it causes in stock are fully related.

5. A fairly complete ecological study of ragwort, showing the effect of climatic, edaphic, and biotic factors on the establishment and distribution of the weed, reveals the biotic factor to be of the greatest importance in its control. The effect of plant competition on the establishment of the seedling is extremely important. Long grass and short continuous turf prevents the establishment of ragwort altogether, while overgrazed pastures, owing to the partial exposure of the soil surface, carry a high infestation of the weed. *Man*, *Insects*, *Sheep*, and *Rabbits* are the chief zoological factors influencing ragwort in this country. The three former are controlling agents, while the action of rabbits in breaking the vegetation cover and exposing the soil, is, in general, distinctly favourable to the increase of the plant.

Owing to the absence of the European insect enemies of ragwort in New Zealand, they are of particular interest from an economic standpoint.

6. Over sixty insects, from five different orders, are recorded from ragwort, and a list of these, with notes on their life histories and alternative hosts, is made.

7. Two insects, the Arctiid moth, *Tyria jacobaeae* L. (cinnabar), and the Anthomyiid seed-fly, *Pegohylemyia seneciella* Meade, because of their extensive damage to the plant and their specific habits, are selected for special study. A number of other insects which cause a small amount of damage, also receive some attention.

8. Details of the life history of *Tyria* are worked out.

9. An account of the parasites reared from the larvae and pupae of *Tyria*, and their percentage infestation is given. This is the first rearing record of *Ichneumon perscrutator* Wsm., a parasite of the pupa.

10. Several fungi, which cause a mortality of 16–20 per cent. in *Tyria* pupae, were cultured and identified.

11. The mortality in the pupae of the cinnabar, due to the action of predators is found to be very high—about 60 per cent. Evidence points to the mole as the chief culprit.

12. An account is given of the life history, synonymy, and parasites of *Pegohylemyia seneciella* Meade. The mouth-parts and spiracles of the larva are figured.

13. The following species of insects cause a small amount of damage to ragwort: *Agromyza aeneiventris* Fln. (dipterous stem-borer), *Homeosoma nimbella* Dup. (lepidopterous stem-borer), *Phytomyza atricornis* Mg., and *Spilographa zoe* Loew. (leaf-miners), *Sphenella marginata* Fln. (flower-head fly), and *Aphis jacobaeae* Schr. A short account of the damage caused by these and the parasites reared from some of them is given.

14. A census of the ragwort and *Tyria* populations is made in several areas, and the methods employed described. Notes are made on the very extensive damage caused to the weed by the larvae of *Tyria*.

15. It is found that ragwort reacts to insect attack by producing a secondary crop of flowers and seeds. This reaction reduces the effectiveness of controlling insects. The whole of this aspect of the problem, showing how weed control by insects is more difficult of attainment than insect control by means of their entomophagous enemies is discussed.

16. Extensive experiments on the effect of cutting the whole plant or different parts of the plant, to simulate insect attack, were carried out. The following conclusions confirmed by observations on actual insect attack were reached:

(*a*) A badly attacked plant, if originally vigorous and if the growing season is good, has enough reserve energy to produce a second crop of seeds equal to 34·7 per cent. of the original potential yield producible in the absence of attack, thus reducing a total loss of 100 per cent. to one of 65·3 per cent.

(*b*) Plants with little or no reserve energy, growing on very poor soil, when badly attacked, do not produce seeds secondarily.

(*c*) Many plants which are unable to produce a second crop of flowers and seeds in the year of attack, may send out small shoots from the base of the stem. These shoots grow vigorously in the following year and are often capable of producing more seed than the original plant. Field observations show that this method of secondary growth has the effect of prolonging the life of the plant beyond the ordinary biennial period.

(*d*) Damage to any part of the plant (leaves, stem and flowers) will lower the seed yield for that season.

17. It is shown that *Tyria*, under certain conditions and in certain areas, has a controlling effect on ragwort in Britain, but in a wide, sandy area, like the Breckland of Norfolk, on account of its distribution not being uniformly general, it is less effective.

18. *Pegohylemyia seneciella*, in the south of England, infests 8–9 per cent. of the capitula of ragwort, and each larva destroys 75 per cent. of the seeds in the capitulum which it occupies. In the North of Scotland it is much more effective, 33–34 per cent. of the capitula being attacked.

19. The areas in England where some degree of control has been effected, are described for the purpose of comparison with conditions prevailing in the ragwort areas of New Zealand. The importance of eliminating factors, such as rabbit activity and overgrazing by farm animals, which predispose to open soil conditions, is strongly emphasised.

20. Indications of the future progress of the work are given, but it is too early yet to foretell the ultimate results of the researches.

21. Other methods of control—cultural, grazing, and chemical are described.

22. Details of collecting and shipping the controlling insects are given. In all 633,289 individuals were exported to New Zealand.

23. An extensive bibliography on weed control is appended.

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A STUDY OF THE NATURAL CONTROL OF THE PEA MOTH, *CYDIA NIGRICANA*, STEPH.

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(PLATES VII and VIII.)

CONTENTS.

1. Introduction.

The moth, *Cydia nigricana*, Steph., whose larvae feed within the pods of growing peas, is considered by some authorities to be one of the principal pests of agriculture in Canada. It is particularly troublesome in the Maritime Provinces, parts of British Columbia, and Ontario. Indeed, so great was the damage it occasioned in the latter district, that farmers found it impossible to grow the main mid-season crop of peas with any hope of a profit. Such extreme abundance is said to be due to the absence of natural enemies, which did not accompany their host when it was accidentally introduced from Europe into the Dominion. This unfortunate event occurred as far back as 1893, and since then the insect has had ample time to make the best of the favourable conditions existing in its new environment, with the deplorable results already mentioned. As the obvious remedy for a pest of this nature consists in the importation of the most suitable and most effective of these natural enemies from the original home of the moth, it was decided that a study of the insect, and the factors affecting its control, should be undertaken by the writer in England. The results of this investigation are set down in the following pages.

The paper opens with a general account of the biology of the pea moth, and this is followed by an analysis and description of the chief restrictive agencies which are associated with it in this country. These agencies include insect parasites of the superfamily ICHNEUMONOIDEA, Nematode worms, entomophagous fungi, and climatic factors, such as rainfall, sunshine, and temperature. Because of their greater practical importance, the insect parasites have been given special attention, and the more or less comprehensive account of their biology, developmental stages, and certain other significant features, occupies a large part of the text. Previous attempts to subjugate this pest by the use of chemicals and cultural aids are briefly outlined and examined, and the more or less negative results obtained from these forms of control serve, by contrast, to enhance the prospects for the method advocated in this paper. Several interesting and unusual ways of collecting infested peas were evolved during the course of the investigation, and a short section, which includes an account of the technique used for handling and shipping parasitized material, deals with this part of the project. Finally, the whole problem is reviewed in the light of the knowledge gained, and so far as this is possible, the probable outcome of the work in Canada is indicated.

2. Biology of the Pea Moth.

Systematic Position, Synonymy and Description of Adult.

Cydia nigricana, Steph. (fig. 1, *e*) is a small moth belonging to the family EUCOSMIDAE, superfamily TORTRICOIDEA, and Order Lepidoptera. Its synonyms are as follows: *Laspeyresia nigricana*, Steph., *L. nebritana*, Zell., *L. non*, Treits., *L. pisana*, Guen., *L. proximana*, Wilk., *Grapholitha nigricana*, Tr., *Endopisa nigricana*, Steph.

The adult moth can be recognised fairly easily by its golden-tinted grey-brown colour, and by certain characteristic markings on the forewings. These consist of short, slanting, whitish streaks, or strigulae, situated on the outer costal edge, and a dark-brown wavy line fringed with long, cilia-like scales of a similar colour on the terminal margin. In addition to these, and quite close to the termen, there is a U-shaped area of a shiny slaty-blue colour, inside which there are four or five short, thickish, black lines, and at the open end a pair of oblique strigulae. The ground-colour of the hind wings is more or less similar to that of the fore ones, except that anteriorly they are of a somewhat lighter shade and the fringe of cilia-like scales on the termen is light grey in colour. When fully extended the wings of the female measure 12–16 mm. from tip to tip.

The male is rather smaller than the female and paler in colour, especially in the anterior region of the forewings. It is further characterized by the presence of a dorsal fold, or pocket, lined with hairs, on the hind wings.

Distribution and Host-plants.

According to Meyrick the pea moth is common in Britain up to the Clyde, but the writer, in the course of his work on the insect, found it common on field-crops of peas only in the south-eastern counties of England, chiefly Essex, Suffolk, Cambridgeshire, Huntingdon, and south Lincolnshire. It appears, also, from certain Ministry of Agriculture reports, that it may be found in parts of Lancashire, and it is very likely present in Worcestershire, where large quantities of peas are grown, but these areas have not been worked by the writer, nor have any reports been received from them during the course of this investigation. In north Lincoln and Yorkshire the insect was conspicuous by its absence, and no specimens were received from these areas, except a few from gardens on the Yorkshire coast. Its distribution extends over Southern and Central Europe, Central and Western Asia to northern Persia, and as a result of accidental introduction, certain parts of North America,

notably the Maritime Provinces, Eastern Quebec, Ontario and British Columbia in Canada, and Wisconsin, New York, Michigan and Washington in the United States.

The usual host of the moth is the common edible pea (*Pisum sativum*) both garden and field varieties, but according to Hanson and Webster, sweet peas, vetches, and, to a lesser extent, lupins and brooms may also be attacked.

Life-history.

Several writers (Brittain, Fluke, Miles, etc.) who have experimented with various chemical preparations for the control of this pest have given an account of its life-history and the following summary, which is in agreement with and partly supplemented by my own observations, has been compiled from these sources. The mature larva and pupa, however, have not hitherto been adequately described or figured, so that the matter relating to these stages is entirely new.

A few moths emerge from their cocoons early in June, but the peak of emergence is not reached until the beginning of July, and adults may be taken in the field up to the middle of August. From June onwards the eggs (fig. 1, *a*) are laid singly

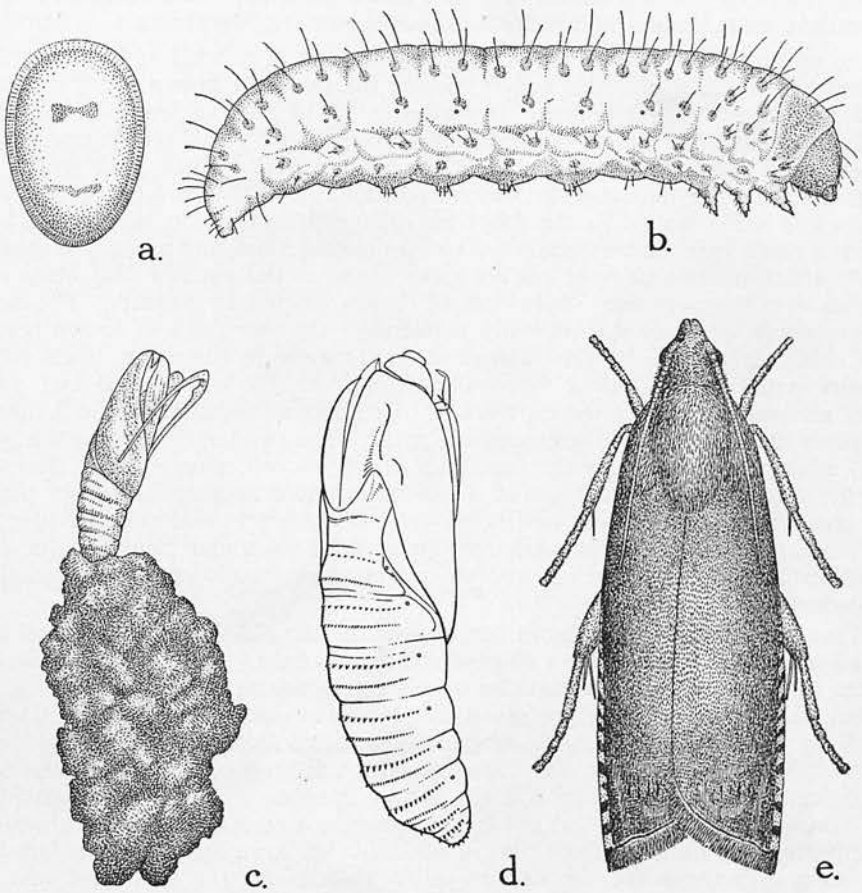

Fig. 1. *Cydia nigricana*, Steph.: *a*, egg (× 35); *b*, mature larva (× 9); *c*, cocoon with empty pupal case attached (× 5); *d*, enlarged view of empty pupal case showing rows of dorsal spines (× 9); *e*, adult moth in resting position showing characteristic wing markings (× 9).

on the sepals of the pea flower, but in captivity they may be deposited indiscriminately on the stems, leaves, petals and sepals. They are rather flattened in appearance, yellowish white in colour, oval-elliptical in shape, and measure 0·75 mm. in length by 0·50 mm. in breadth. At first they are translucent, but after 12 to 24 hours they become obscured by two irregular red streaks, which disappear on the sixth day, when the outline of the larva can be seen through the chorion. The incubation period usually lasts about seven or eight days.

The newly emerged larva is whitish in colour, except for the brown head and dorsal shield of the first thoracic segment, and measures 1·2 mm. in length. It is very active and wanders about for a short time before commencing to tunnel its way inside the pod. Once inside, it proceeds to eat the young peas and in the course of a larval life of about three weeks duration, it makes a large number of surface excavations on the majority of the seeds. On and around the damaged peas it deposits a considerable quantity of frass, in the form of small pellets webbed together with silken threads, which gives the infested pod a very characteristic appearance (Plate VII). Normally there is only one larva in a pod, but sometimes two are found, and very occasionally three, in which case there is usually a marked difference in the individual ages of the several larvae. In the course of its development within the pod the larva moults four times and passes through five stadia.

The mature larva (fig. 1, *b*), which is composed of a head and thirteen body segments, is yellowish white in colour, except for the light brown head and dorsal shield of the first body segment. It measures 13–15 mm. in length. Useful distinguishing characters for this stage are the brown dorsal shield on the first thoracic segment, and the large number of light brown subcircular areas, from which pale-coloured hairs arise, situated in various positions over the surface of the body. These areas are arranged in the following order: Dorsally—on segments 2 and 3 there is a single pair, each of which has two projecting hairs, and on each of segments 4 to 11 there are two pairs of smaller areas, those of the anterior pair being closer together than the posterior; from each of these a single hair projects. The dorsum of segment 12 is somewhat generally pigmented, the two pairs of brown coloured areas being placed side by side instead of one anterior to the other, while the last segment—number 13—has a triangular-shaped, lightly coloured dorsal surface with a number of hairs projecting from it. Laterally on segments 2 and 3 there are four pigmented areas, three large and one small. The two larger have each a pair of hairs, while the third has only one, and the small one none at all. Above the spiracles on segments 4–11 there is a row of indented subcircular brown patches, each patch with a single hair, and below them there is a row of more circular areas each with two hairs. Underneath this latter infra-spiracular row there is a final line of smaller spots, the first of which on segment 1 has two hairs, and the remainder, on segments 2–11, only one.

When fully matured the larva cuts a hole in the side of the pod, drops to the ground and enters the soil for a short distance in order to spin its cocoon (fig. 1, *c*). During the spinning process particles of soil get incorporated with the silken fibres so that the cocoons, which are of an elongate-oval shape averaging 9–10 mm. in length by 4–4·5 mm. in breadth, ultimately come to look like small lumps of soil from which, at first glance, they are not easily distinguished. The inner cocoon proper, consisting mainly of spun fibres, is grey in colour and of a tough parchment-like consistency. At this point the larva undergoes a certain amount of change and its appearance is different from that of the fully fed larva before cocoon formation. The main differences are the deeper yellow colour and the shortened and more distended body. In this stage the insect passes the winter.

Pupation takes place in June, or in some cases towards the end of May, and this instar lasts just under a fortnight. The pupa is dark brown in colour and measures 6 mm. in length by 1·8 mm. in maximum breadth. It is characterized by double

rows of strong reflexed dorso-lateral spines on all the abdominal segments, except the last three, which have only a single row each (fig. 1, *d*). On those segments with double rows the spines of the front row are fewer and stronger than those of the back one. Some little time before the formation of the pupa, the resting larva loosens the tightly spun fibres at the head end of the cocoon, and these loosened fibres may be pushed out a little way so that the cocoon comes to be much longer than usual. Through this weak spot the pupa pushes its head and wriggles out with the help of the spines already described. The last few abdominal segments are not usually withdrawn from the cocoon, and empty pupal cases attached in this manner have been found in considerable numbers in the rearing tins (fig. 1, *c*). Apparently when deeply buried in the soil the larva cuts its way out of the cocoon and comes up to the surface in order to pupate. A few empty unattached pupal cases were occasionally found, but the former method of emergence was the most usual one.

3. Factors of Natural Control.

In England two main types of controlling factors, one physical and the other biological, influence the numbers and distribution of the pea moth. The principal constituent of the former is climate, which acts both directly on the insect itself and indirectly through the host-plant; while the main components of the latter are: (1) parasitic insects; (2) parasitic Nematode worms; (3) entomophagous fungi. As a result of the action of these factors not more, on the average, than 10 to 16 per cent. of the pods were attacked by the pea moth in the south-eastern counties of England during the years 1935–37. This estimate, if anything, errs on the high side, because when making collections of this kind one naturally tends to select the most heavily infested material, so that an unbiased census of the population would almost certainly give a lower figure, probably one not above 10 per cent. It is true that in parts of Essex, where conditions appear to be specially favourable, much higher percentages were from time to time obtained, but the statement of a leading canner—" This insect does not worry us in this country "—appears to represent the situation fairly well, at any rate during the years under review. Although from an analytical standpoint climate naturally takes precedence over the biological agencies, yet it is a factor which lies beyond the control of man and is therefore regarded, from the practical point of view underlying the present investigation, as being of more or less secondary importance. Because of this the short general statement on its effects follows the account of the biological factors. Of these latter, the parasitic insects are considered to be by far the most important, both because of the reduction in the numbers of the host population which is effected as a result of their activities, and because it has been found possible to utilise them in a practical manner for the control of this pest.

Parasites.

Parasites recorded and reared.

In the literature, three parasites of the pea moth are recorded from Continental areas, but none from England. They are as follows:—

1. *Ascogaster quadridentatus*, Wesm. (Braconid). Recorded by Marshall (1888) as a parasite " avec plus de certitude " of, amongst other Lepidoptera, *Endopisa nigricana*, Steph.
2. *Glypta haesitator*, Grav. (Ichneumonid). Recorded by Morley (1908) as being bred by Brischke in Prussia from *Grapholitha nebritana*.
3. *Epiurus* (*Pimpla*) sp. (Ichneumonid). Recorded by Schutze and Roman (1931) from, among other species, *Grapholitha nigricana*.

From the material collected by the writer in the south-eastern counties of England during the years 1935–37, the first two parasites, *Ascogaster quadridentatus* and *Glypta haesitator* were reared in considerable numbers, and a few specimens of a new and hitherto unrecorded parasite, *Angitia* sp., were also obtained. So far as I am aware, this is the first time that these three parasites have been reared from the pea moth in this country. The species of *Epiurus* mentioned by Schutze and Roman was not bred out, and it is probable that this is a rare and occasional parasite on this host, unless, of course, it is a purely continental species, which seems unlikely.

Ascogaster quadridentatus, which oviposits in the egg of the pea moth and the larva of which develops in the host caterpillar, was found to be the most abundant parasite. During the years 1936–37 an average of 36–45 per cent. of the host larvae were parasitized by this species, the maximum number being 48 per cent. *Glypta haesitator*, a purely larval parasite, accounted for another 12–14 per cent., with a maximum of 24 per cent. ; while *Angitia* sp., also a parasite of the larva, with 2 per cent., or less, was comparatively rare. From the three species combined the greatest amount of parasitism obtained was 60 per cent.

Keys to Adult and Developmental Stages.

Key to Adults.

1.—Forewings with only one recurrent nervure, Braconid type of venation ; dorsum of abdomen in form of a carapace or shield, without any visible sutures (fig. 2, *b*).....*Ascogaster quadridentatus*

Forewings with two recurrent nervures, Ichneumonid type of venation.....2

2.—Abdominal segments 2–4 with oblique impressions converging anteriorly (fig. 2, *a*) and segments 1–4 black with reddish posterior margin, remaining segments black ; abdomen unpetiolated, not compressed laterally ; forewings without an areole .....*Glypta haesitator*

Abdominal segments without oblique impression and black without a reddish margin ; abdomen markedly petiolated and compressed laterally ; areole present in forewing.....*Angitia* sp.

Key to Primary Larvae.

1.—Head more or less quadrate or only lightly chitinized ; first body segment large and prominent ; proctodaeum evaginated from last segment, forming in the older primary larvae a more or less circular anal vesicle.....
Ascogaster quadridentatus

Head elongated, bullet-shaped, well chitinized ; first body segment not more prominent than following ones ; last body segment prolonged into a tapering tail 2

2.—Paired projections or protopods present ventrally on segments 1–12 ; paired dorsal grooves on head ; tracheal system fairly well defined with two longitudinal extensions into the tail.....*Angitia* sp.

Protopods absent ; head without dorsal grooves ; no evidence of tracheal system .....*Glypta haesitator*

Key to Mature Larvae.

1.—Mandibles toothed, labial ring somewhat quadrate in shape ; medium and very large spines (64–72 μ) present on dorsum as well as small tubercles (fig. 7, *a*, *b*) ; atrium of spiracle oval, 25–36 μ diameter.....*Ascogaster quadridentatus*

Mandibles not toothed, labial ring subcircular.....2

2.—Labial ring very much thickened ventrally ; chitinized Y-shaped area within latter ; maxillae with chitinized border ; mandibles rather small, 0·09 mm. in length ; spiracles minute, diameter of atrium 14 μ (fig. 7, *f*).....*Angitia* sp.

Labial ring not thickened ventrally ; chitinized Y-shaped area absent ; maxillae unchitinized ; mandibles fairly large, 0·12 mm. in length ; spiracles large and well developed, diameter of atrium 25–38 μ (fig. 7, *g*).....*Glypta haesitator*

Key to Cocoons.

1.—Cocoon with a white circular band round the middle.....2

Cocoon without a circular band, white, thin, and translucent (fig. 8, *a*)..... *Glypta haesitator*

2.—Cocoon, apart from broad white circular band (1·7 mm. broad), pale glassy white (fig. 8, *b*).....*Ascogaster quadridentatus*

Cocoon, apart from narrow white circular band (0·5 mm. broad), dark brown to black ; black band on interior surface of cocoon.....*Angitia* sp.

Note on Structure of Cocoons.

The manner in which the cocoons of the different parasites are constructed is rather interesting. In all three species there is an outer covering of loosely woven fibres easily removable from the main body of the cocoon. This is followed by one or more inner layers of a stronger and tougher consistency. *Glypta* has only one of these, which is thin, transparent, and shiny ; *Ascogaster* has three of a similar type, all adhering very closely to one another ; and *Angitia* has one, of a dark brown colour, with a dark circular band in the middle, and two which are light brown and of a very fine texture.

Glypta haesitator, Grav.

This parasite is not quite so common on the pea moth as *Ascogaster quadridentatus*, but since a rather full account of its bionomics, developmental stages, etc., has been prepared it is given precedence in the text.

Percentage Attack in S.E. England.

TABLE I.

Year	Area	Parasitism per cent.
1935	Wisbech, Cambridgeshire	14
,,	Huntingdon	12
,,	Graveley, Cambridgeshire	12
1936	S. Lincoln, 1	20
,,	Essex, 1	16
,,	Farnham Royal, Bucks	13
,,	S. Lincoln, 2	12
,,	Suffolk	8
,,	Emneth, Cambridgeshire	6·6
,,	Essex, 2	0
,,	Honeydon, Bedfordshire	0
,,	Great Shelford, Cambridgeshire	0
1937	Threekingham, S. Lincoln	24
,,	Essex, 3	15
,,	Essex, 2	10
,,	Essex, 1	7

From the above table it will be seen that *G. haesitator*, although apparently absent from one or two areas is, nevertheless, fairly evenly distributed over the pea-growing districts of South-East England. As already stated, its average percentage parasitism during the three years under review was 12–14 per cent., and its maximum 24 per cent.

Systematic Position, Host Records and Distribution.

This species belongs to the family ICHNEUMONIDAE, subfam. PIMPLINAE and tribe GLYPTINI. According to Schmiedeknecht, the chief characteristics of the GLYPTINI are, the long narrow unpetiolated abdomen and the paired oblique

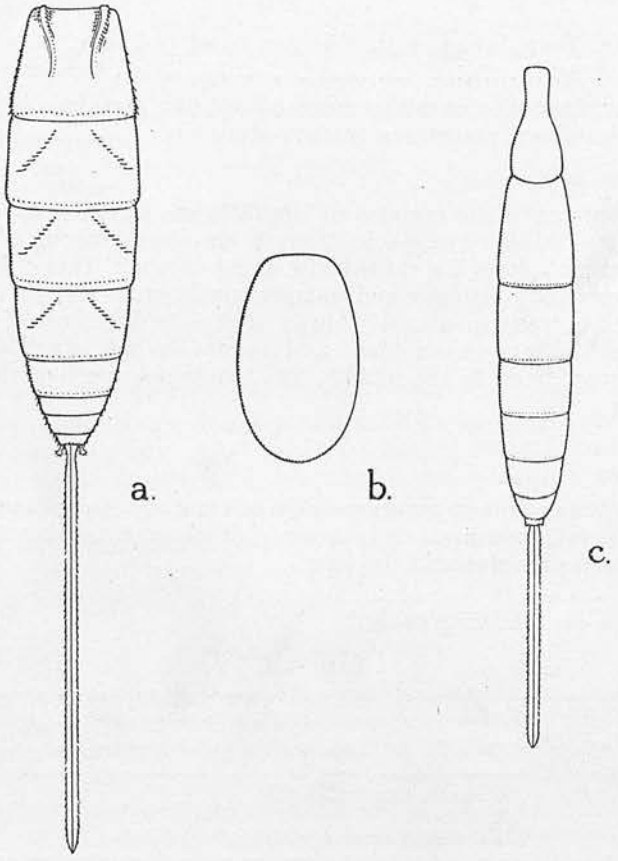

Fig. 2. Abdomen of: *a*, *Glypta haesitator*, Grav. ♀ (note oblique impressions and gastrocoeli); *b*, *Ascogaster quadridentatus*, Wsm. ♀ (note absence of sutures); *c*, *Angitia* sp. ♀; (all × 15).

impressions which converge anteriorly on the second, third and fourth abdominal segments (fig. 2, *a*). Transverse impressions such as occur in the LYCORINI, the most nearly related group, are absent. A further distinction between these two tribes is to be found in the scutellum, which in the GLYPTINI is rounded posteriorly, nd in the LYCORINI is quadrate. The genus *Glypta* itself exhibits all the characters of the tribe to which it belongs and in addition has the distinction of being without an areole on the forewing. Fifty-six known species are listed by Schmiedeknecht (1933). In order to form some idea of the host relationships of this genus, the

extensive card index catalogue at Farnham House Laboratory was examined for host records. In all 118 such records were obtained. Ninety-three of the hosts are members of the subfamily TORTRICOIDEA, which is a group of small moths more or less characteristic of the temperate regions, and the chief genera attacked are *Cydia*, *Tortrix*, *Rhyacionia*, *Argyroploce* and *Epiblema*. The members of these genera, in common with most of the TORTRICOIDEA, are usually either leaf-rollers, stem-borers, fruit-feeders, or feeders inside seed-pods, and all may be classified as internal feeders. It is thus interesting to learn that the hosts of the various species of *Glypta*, although so numerous, are fairly closely related both systematically and ecologically.

The only host records of *haesitator* itself, other than the pea moth, are those of Bignell's, who reared it from the Eucosmid, *Spilonota ocellana*, Fab., which feeds on blackthorn, apple, larch and alder, and of Morley, who states that Lord Walsingham bred it from a *Tortrix* larva on *Myrica gale*.

Records of distribution mention only three countries, Sweden, Germany, and England, although it is quite possible that it occurs over a much wider area.

Description of Adult Parasite.

Average length.—Female, including ovipositor, 8·5 mm. (excluding ovipositor 5·5 mm.), male 6·5 mm. *General colour*—head, thorax and abdomen mainly black, except for narrow reddish markings on the posterior border of the first four abdominal segments. Legs mainly reddish. *Head*—somewhat rectangular in the female, about 2½ times as broad as long, square in the male, black, shiny, strongly punctate, with covering of fine white hairs especially long and marked in and around the clypeal region, palpi mainly straw-coloured with basal parts dark brown. Three prominent ocelli on vertex. *Eyes* fairly large, dark brown. *Antennae*—dark brown to black, lightly pilose, filiform. Flagellum of 33 joints in female, 36 in male. Flagellar joints covered with whitish, narrow, elongated areas, probably sensory in nature ; remainder of antenna consists of small basal joints the first being slightly larger than the second. *Thorax and propodeon*—black, punctate, shiny, notauli rather faintly marked, mesoscutellar area at side deeply excavated and striated, metanotum similar, with small raised portion in centre ; fielding on propodeon somewhat reduced, costulae absent, spiracles small, subcircular and inconspicuous, pleural region of propodeon very hairy. *Wings*—hyaline, hairy, areole absent, tegulae pale yellow. *Legs*—(female) anterior and middle legs (save for coxae and first trochanter joints, which are mainly black) reddish. Main part of femur and middle part of tibiae of posterior legs reddish, remainder of tibiae black, except for white basal area. Tarsi of posterior legs black, save for light basal areas on segments 1, 2 and 3. Pulvilli black, last tarsal joint of middle legs dark brown. Single basal spur on tibiae of first pair of legs, two on middle and posterior legs. Male differs from female in having the tarsal joints of the middle legs dark brown, except for a light basal area. *Abdomen* (fig. 2, *a*)—black with posterior margins of first four segments reddish, eight segments visible dorsally, strongly punctate, faintly pilose, two strong dorsal carinae on segment 1 extending from anterior margin of the segment to a little way beyond the middle, on segments 2, 3 and 4, a pair of oblique impressions, which converge anteriorly, ovipositor about same length as abdomen.

The male is easily distinguished from the female by the absence of an ovipositor, by the number of joints in the flagellum—36 in male, 33 in female—and by the less conspicuous reddish bands on the abdominal segments.

General Bionomics.

The imago of *G. haesitator* emerges from the overwintering host cocoon towards the end of June and the beginning of July. Males appear a few days before the females and the sex ratio is 0·5, or two females to one male. Mating is a simple affair and takes place soon after emergence. In one instance the male in his excitement was observed to make several abortive attempts to mate with the head of the

female, but very soon copulation was effected in the normal way, the male holding on lightly to the wings and abdomen of the female, and his abdomen curved round with the tip underneath hers. During coition the antennae of both sexes were held more or less erect and vibrating rapidly. The whole performance lasted only about three-quarters of a minute. On the 1st July 1936, a mated female was placed in a cage containing a number of pea-pods, the majority of which were known to be infested with the larvae of the pea moth. Very soon she took an interest in them and began to sense their shape and to explore their surface with her antennae. These were curved round at the tip so that the upper surface, which by means of the curvature was now directed downwards, could be used for searching purposes. The lower surface was also employed but only occasionally. When really excited she curved her antennae for as much as half their length and tapped them rapidly. After this preliminary examination the ovipositor was withdrawn from its sheath and bent forward at an acute angle underneath the abdomen until it was almost parallel with the body. It was then inserted into the pod and a single egg laid in the pea moth larva inside. Whether the parasite stung the host larva through the hole which the latter made when entering the pod, or whether it made a fresh hole of its own, was not determined, but it seems much more probable that it adopts the former course, especially since in the earlier part of the season, only the younger pea moth larvae were found to be parasitized. This suggests that the entrance hole of the host remains open for some little time after the latter has gained access to the pod, and if the parasite does make use of the tunnel, these early stages would get parasitized, while the older larvae, because of the closing of the hole by the growth of the tissues, would escape. Support is given to this explanation by the fact that an allied species, *Glypta rufiscutellaris*, also oviposits on the early stages of its host, *Cydia molesta* (the oriental fruit moth), and only through the entrance hole which the latter makes in the peach stems on which it feeds (Montgomery, 1935).

Intense positive phototropism was exhibited by the adult parasites while they were confined in the rearing cages in the laboratory.

The egg is laid internally in the host larva and hatching takes place about three to four days after oviposition, when a typical internal Ichneumonine first-instar larva, with a blunt bullet-shaped head, a cylindrical body and a tail, emerges. During the rest of the summer the parasite remains in this stage, but in the autumn it moults, and the second instar, which is the stage present in the host larva throughout the winter, makes it appearance. Two further ecdyses take place, one in February and the other towards the end of May, so that in all there are four instars in the larval stage. When it has entirely devoured the contents of its host the mature larva sheds the skin of the latter and begins to construct a cocoon. This is made of white translucent silk and differs from that of the other parasites in not having a median circular band. The insect now passes a few days as a prepupa, and before the final ecdysis into the pupal stage, the faeces, which have accumulated and been retained in the gut during the feeding period, are voided. At a temperature of 25°C. and relative humidity about 60 per cent., the pupal stage lasts for seven days. After emergence the imago, with proper care and attention, can be kept alive in the laboratory for the comparatively long period of three weeks to a month.

Description of Developmental Stages.

It will be noted in the following pages that a good deal of prominence is given to certain larval structures, such as the cephalic skeleton, the respiratory system, and the skin armature. In explanation it may be stated that these structures and the variations which occur in them are the most useful and perhaps the only characters which can be used for distinguishing the various parasites in the larval stages.

The *egg* (fig. 3, *a*) is whitish in colour, slightly shiny and of an elongated sub-reniform shape, with one end broader than the other. Length 0·44 mm., maximum breadth 0·08 mm.

The *first stage larva* (fig. 3, *b*) is of the usual characteristic internal Ichneumonine type. It consists of a long narrow bullet-shaped head and a cylindrical body of thirteen segments, the last of which is prolonged into a tail with a slight dorsal tilt at its posterior end. The cuticle of the head is chitinized and brown in colour, while the body is soft, smooth, colourless and transparent, so that the internal organs are clearly visible through the integument. When fully grown the first stage larva is about 1·5 mm. in length. In front view the cephalic skeleton of the head (fig. 4), as we may call the whole arrangement of chitinized parts consisting of mandibles and associated structures around the mouth, is seen to be fairly well differentiated. The pointed mandibles articulate above with a condyle on the short

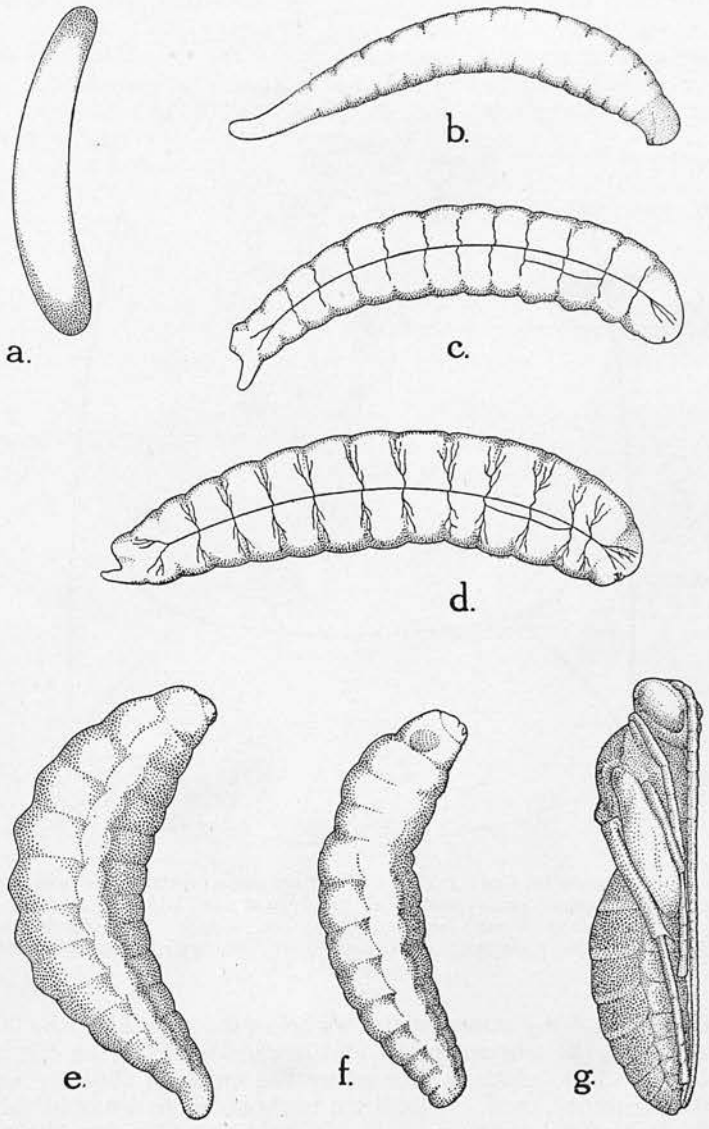

Fig. 3. *Glypta haesitator*, Grav. : *a*, egg (× 110) ; *b*, 1st stage larva (× 45) ; *c*, 2nd stage larva (× about 18) ; *d*, 3rd stage larva (× about 18) ; *e*, mature larva (× about 9) ; *f*, prepupa (× about 9) : *g*, pupa (× about 9).

superior mandibular strut, and below with the unusually large inferior mandibular strut. This latter is formed of a broad band of lightly chitinized tissue folded and strengthened on its outer edge and produced inwards to join with its fellow of the other side. Centrally this compound bar is hollowed out to form a subcircular labial area in which the thin bilobed labium can be discerned. The superior and inferior mandibular struts are joined together by the two arms of the pleurostoma, one on each side of the mouth, and this is continued upwards above the clypeus to form the epistoma. Other prominent structures present in this stage are, the clypeal arch on the border of the clypeus, and the chitinized trough of the pharynx, which is more apparent in side view. Less prominent features are the paired maxillae,

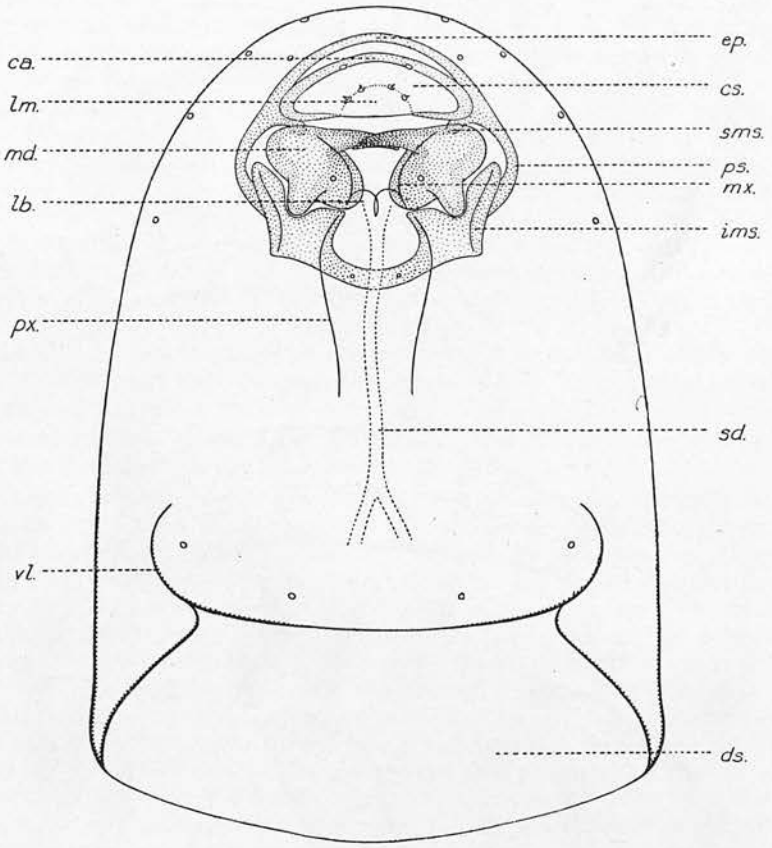

Fig. 4. *Glypta haesitator*, Grav. : head of 1st stage larva, ventral view, showing cephalic skeleton : *ep*, epistoma ; *ca*, clypeal arch ; *cs*, clypeus ; *lm*, labrum ; *sms*, superior mandibular strut ; *ps*, pleurostoma ; *md*, mandible ; *mx*, maxilla ; *ims*, inferior mandibular strut ; *lb*, labium ; *px*, pharynx ; *sd*, salivary duct ; *vl*, ventral lobe ; *ds*, dorsal surface of head ; (× 750).

which consist of thin fleshy transparent lobes below the mandibles, the bilobed labium already mentioned, the labrum (below and marked off from the clypeus), and the common salivary duct, which is formed by the union of the two separate ducts just after they enter the head. In addition to these organs a number of conspicuous setae are situated on the cuticle in and around the mouth region, five pairs towards the pleural edge of the head and two pairs at the postero-ventral border in the region of the ventral lobe. In side view the antennae near the anterior end of the head can

be discerned, as well as the floor of the pharynx, which is chitinized for a considerable distance behind the mouth. There is no visible trace of a tracheal system in this stage.

The *second stage larva* (fig. 3, *c*) is quite different in appearance from the first. Most remarkable are the differences in the head and the tail. The former is characterised by a pair of large cerebral ganglia, by the absence of the brown chitinization which was so prominent in the first stage, and by the roughly hemispherical shape, as well as the longer and flatter ventral lobe, and a slight indentation dorsally. Instead of being a continuation of the last segment along the central axis of the body, the tail is now ventral in position, and only one-eighth of the body length, as compared with one-fifth in the first instar. The upper part of the last body segment containing the posterior end of the rectum is also bent upwards in a characteristic manner. As before, the larva consists of a head and thirteen body segments, the first three of which differ from the remainder by the presence of a small ventral lobe. The tracheal system, which was absent or unmarked in the first stage, is now fairly conspicuous, although it is apneustic without any trace of spiracles.

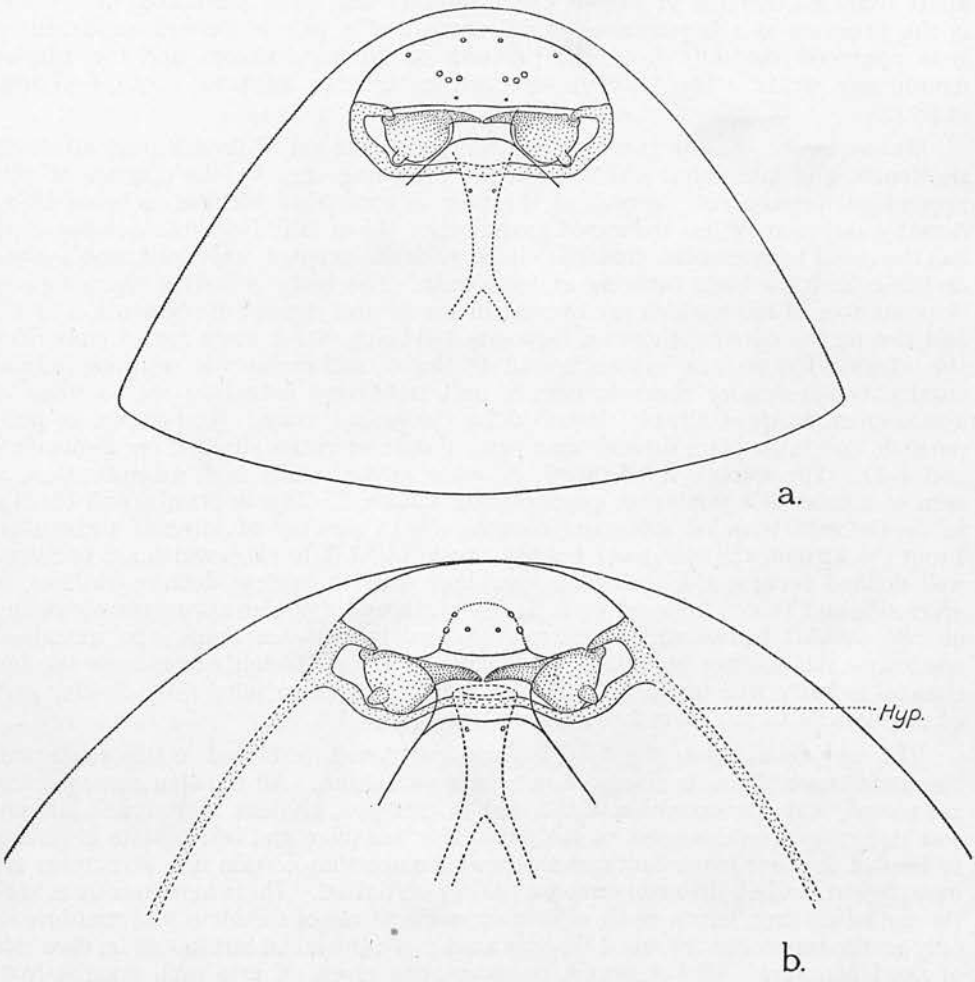

Fig. 5. *Glypta haesitator*, Grav. : cephalic skeleton of : *a*, 2nd stage larva (× 310) ; *b*, 3rd stage larva (× 155) ; *hyp*, hypostoma.

It consists of two longitudinal trunks with two short accessory branches in the thoracic region. The two main trunks are joined together in the first segment by a transverse commissure from which short branches are given off to the head. Further transverse branches are emitted from the longitudinal trunks near the anterior margins of the body segments. The cuticle of the body is more or less transparent, and the yellow gut and white fat-body can be seen through it. In this stage the cephalic skeleton (fig. 5, *a*) is not very well developed, and is only weakly chitinized, but in outline it is similar to that of the first stage. The inferior mandibular struts are now very much narrower and comparatively inconspicuous, the epistoma has almost disappeared or is represented only by a thin weak line, and there is no clypeal arch. The fully grown second stage larva measures 3·5 mm. in length.

The *third stage larva* (fig. 3, *d*) differs from the previous one in several respects. The tail has been considerably reduced (only $\frac{1}{21}$ of the body length), and the upper part of the last body segment, with the posterior part of the rectum, now occupies the normal position. Although still apneustic the tracheal system is better developed and more conspicuous. The main difference in the cephalic skeleton (fig. 5, *b*), apart from the increase in size of the mandibles and other associated structures, is the presence of a hypostoma, which consists of a pair of curved unpigmented rods produced ventrally from the junction of the pleurostoma and the inferior mandibular struts. The fully grown third instar larva measures about 4·03 mm. in length.

Mature larva : At the third ecdysis the larva gets rid of its tail, and although the fourth and last instar differs from the preceding ones by the absence of this appendage, yet the last segment of the body is somewhat peculiar in being tilted dorsally and more or less truncated posteriorly. When fully fed this stage (fig. 3, *e*) has the usual Ichneumonid grub-like shape, with an inconspicuous head, and a more or less cylindrical body tapering at both ends. The body is further characterised by a number of lobes which are present in the pleural regions of segments 2 to 10, and also on the dorsum, those on segments 4–8 being rather more conspicuous than the others. The tracheal system is well developed, and consists of two longitudinal trunks, two accessory thoracic trunks, and transverse branches, etc., similar in arrangement to those already described for the second stage. Respiration is peripneustic and takes place through nine pairs of open spiracles situated on segments 2 and 4–11. The spiracle itself (fig. 7, *g*), when viewed under high magnification, is seen to consist of a somewhat quadrangular atrium, 25–28 μ in breadth and 18–21 μ in depth, with rounded sides and corners, and a number of internal trabeculae. From the atrium, the spiracular trachea, made up of 9–10 rings which are not very well defined because the trabecular markings tend to confuse definite outlines, is given off, and this is followed by a lightly chitinized valvular apparatus consisting of two ovoidal bodies with a narrow channel in between them. In unstained specimens this closing apparatus is difficult to see, although the narrow median channel is fairly well marked. A further length of trachea joins this valvular part of the spiracle to the main longitudinal trunk.

The cephalic skeleton (fig. 6, *a*) is particularly well developed in this stage, and the significance of this is discussed in a later paragraph. All the structures present are paired, with the exception of the median epistoma, clypeus, labrum and labium, and the general arrangement of the mandibles, maxillae and other parts is similar to that in the first instar larva, with the difference that certain new structures are now present, and all the main ones are heavily chitinized. These new structures are : (1) the labial ring, which is an almost complete circle of chitinous material broken only at the top in the region of the spinneret ; (2) the labial struts, one on each side of the labial ring ; (3) the maxillary struts, one given off into each maxilla from the top end of each hypostomal arm ; (4) the oblong-shaped ring in the labial area surrounding the opening of the old salivary duct, which has now been transformed

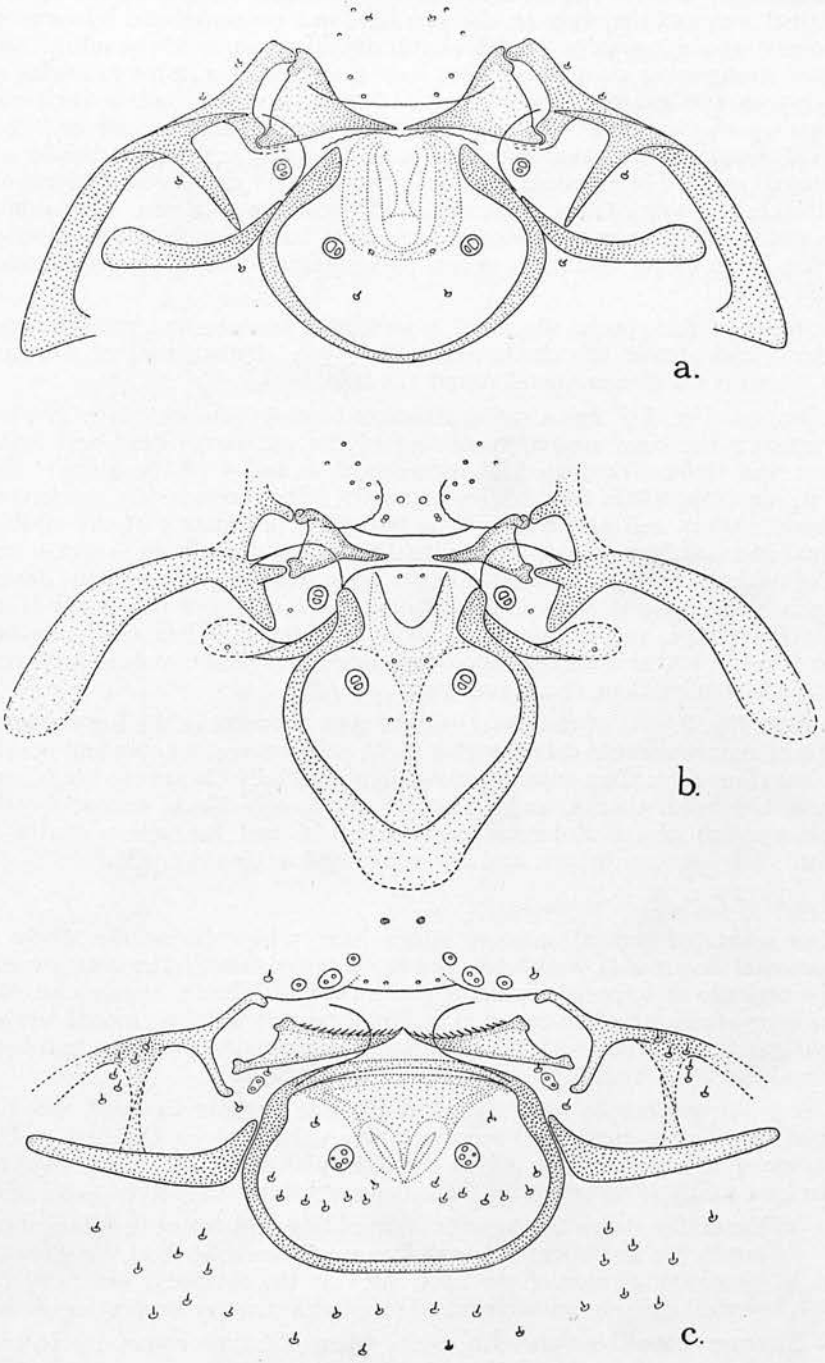

Fig. 6. Cephalic skeleton of mature larva of *a*, *Glypta haesitator*, Grav. ; *b*, *Angitia* sp. ; *c*, *Ascogaster quadridentatus*, Wsm. (all × 155).

into a spinneret ; and (5) the 8-shaped sensory papillae, which are situated one pair in the labial area and the other on the maxillae, and are considered by some writers to be somewhat analogous to the labial and maxillary palps of the adult. A large number of strong setae are also scattered over the facial area in the following order : on the clypeus, two groups of three ; on the labrum, two pairs ; one on each maxilla ; one below each labial strut ; a pair within the labial ring ; a pair on the lower sclerotized margin of the spinneret ; and a final pair on the outside border of each pleurostomal arm. The antennae are fairly conspicuous and in top view are seen to be built up in the form of concentric circles. There is no epistoma. The skin of the body is covered with minute tubercles somewhat triangular in shape, interspersed with a few much longer and more or less pointed spines which have a circular base (fig. 7, *d*).

The *cocoon* of this species (fig. 8, *a*) is somewhat tenuous and translucent. It is rather large and almost fills the cocoon of its host. Unlike that of *Ascogaster* or *Angitia*, there is no circular band round the middle.

The *prepupa* (fig. 3, *f*) has a rather characteristic appearance. It is divided into three regions : the head region, consisting of the old larval head and first body segment ; the thorax, composed of segments 2, 3 and 4 of the larva ; and the abdomen, consisting of the 9 remaining segments. These regions are the forerunners of the head, thorax and abdomen, of the pupa, and ultimately of the adult. The abdominal segment is truncated, and slightly inclined dorsally in a similar manner to that of the mature larva. A further characteristic of the prepupa is the developing eye, which is clearly visible in the head region. The colour of this instar is whitish with a yellow tinge, and its length is about 5·85 mm. When newly formed the prepupa is much longer than the succeeding stage, but before moulting it contracts and becomes smaller than the actual pupa.

The *pupa* (fig. 3, *g*) is of the usual exarate type common in the ICHNEUMONIDAE. At first it is mainly white in colour with a slight yellow tinge, the eyes and ocelli being brown, but three days after pupating the colour gradually changes to black, and two days later the head, thorax, and abdomen are mostly black, except for the red posterior margins of the abdominal segments 1–4, and the yellow centre of the abdomen. The legs are brown, and the wings and antennae hyaline.

Significance of Certain Structures.

A few points of general interest which have arisen during the study of the developmental stages of *G. haesitator* may be discussed here. The first is connected with the cephalic skeleton of the larva and its development ; the second with the peculiar elongated head often found in internally parasitic Ichneumonid larvae, and the prolongation of the last segment into a tail which usually accompanies this type of head ; and the third with the respiratory system.

1. It is interesting to note that the cephalic skeleton is much more highly developed, more prominent, and more strongly chitinized, in the first and fourth stage larvae of *G. haesitator* than it is in the 2nd and 3rd instars. Three reasons may be given for its high development in the mature or fourth stage larva :—

   i. In the earlier stages the parasite larva obtains nutriment in a fluid condition, but in the last instar it has to live mostly on solid food, consisting of the remaining tissues of the host, such as the fat-body, etc., and for this work it requires stronger mandibles and a stronger supporting skeleton.

   ii. Stronger mandibles are also useful when the time comes for it to break through, and cast off, the skin of its host.

   iii. The arduous task of cocoon spinning is carried out in this stage.

This latter function is specially provided for by the transformation of the salivary gland and its opening into a silk gland and a spinneret, respectively. In the first

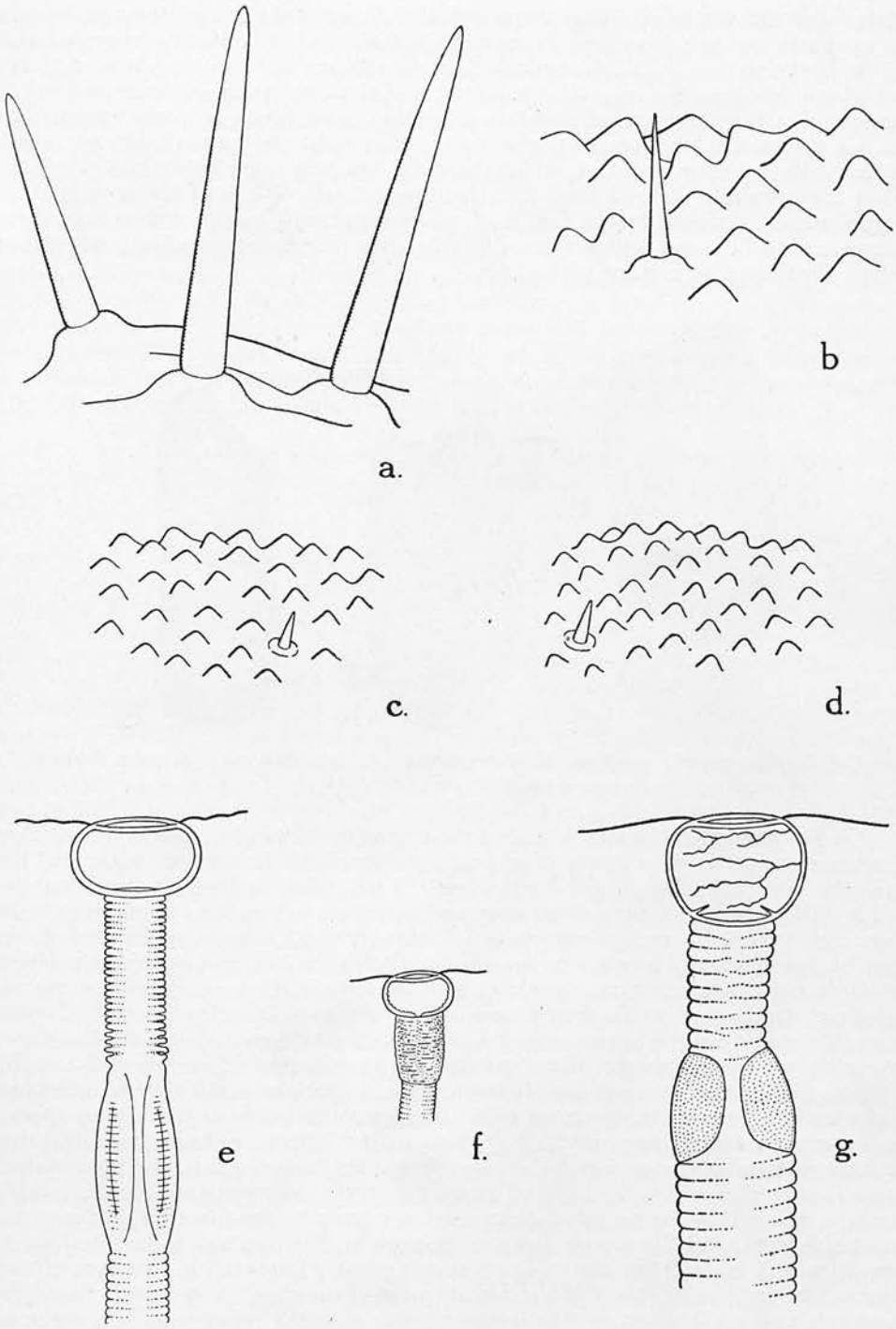

Fig. 7. Skin armature of : *a* and *b*, *Ascogaster quadridentatus*, Wsm. ; *c*, *Angitia* sp. ; *d*, *Glypta haesitator*, Grav. ; spiracles of : *e*, *Ascogaster* ; *f*, *Angitia* ; *g*, *Glypta* ; (all × about 750).

instar it is difficult to see what use a well developed cephalic skeleton can be to a larva unattached to its host, and obtaining its food without any difficulty from the blood of the latter, so that its chief function appears to be one which is associated with the act of eclosion from the egg. In the second and third stages the cephalic skeleton is present, but the parts are only weakly chitinized, from which it would appear that it has no special function to perform save that with each moult the parts get successively larger in preparation for the work awaiting them in the final stadium. That the mandibles are not used for attachment to the tissues of the host in these earlier stages is proved by the fact that, when parasitized hosts are dissected, these stages always float out without any difficulty into the physiological salt solution in which the dissection is being performed.

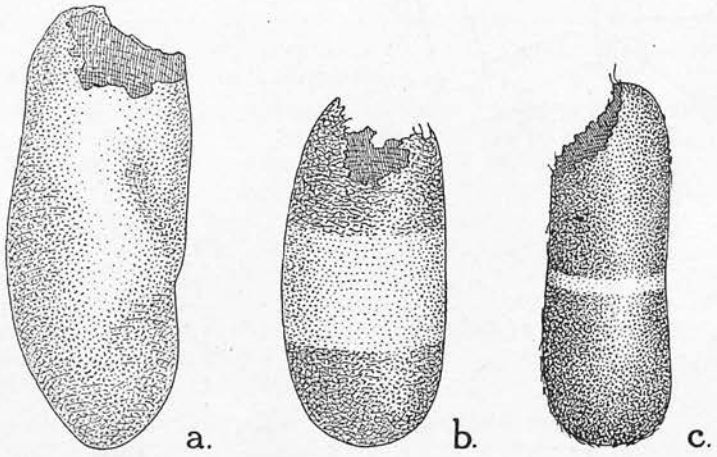

Fig. 8. Cocoons of : *a*, *Glypta haesitator*, Grav. ; *b*, *Ascogaster quadridentatus*, Wsm. ; *c*, *Angitia* sp. (all × about 9).

2. The elongated chitinized head of the first stage larva of *G. haesitator*, which is characteristic of the first instar of so many endoparasitic ICHNEUMONIDAE, and the tail which accompanies it, are interesting. Three different theories involving the tail in duties of a locomotory, respiratory and excretory nature have been put forward from time to time by various writers, but all three of them have been disposed of, the first by the fact that there are no special muscles in the tail, and because the larva, when dissected, shows no movement of a progressive character in physiological salt solution ; the second by Thompson and Parker, whose preparations showed that the internal structure of the tail consists of a lobe of adipose tissue and not of a bundle of tracheids, as the originator of the respiratory theory had supposed, and also by Thorpe, who showed by a number of experiments, in which he used biological indicators (colonies of protozoa) to detect oxygen absorption, that this organ has no special importance in respiration ; and the third because it is difficult to understand why the ordinary method of conserving the faeces in the gut until it is discharged in the prepupal stage is not sufficient for this type of larva as it is for the ectoparasitic species, which have no tail. Thus far no satisfactory explanation as to the function of this organ has been given, and Thompson and Parker came to the conclusion that despite its prominence it is not physiologically of any particular importance. In face of this conclusion, and the rejection of the fore-mentioned theories, the writer hesitates to present a new explanation, but feels nevertheless that the presence of this organ in an endoparasite like *Glypta*, and its absence in an ectoparasite like, for example, *Microcryptus*, has some relation to the medium in which the respective parasites live. He therefore suggests that the tail of the endoparasite is a balancing organ,

which offsets the long heavy head, and keeps the larva orientated in the longitudinal axis of the host's body. In the absence of a tail, it would seem that the head of the parasite would sink in the blood of its host, so that the body of the former would come to lie in a position more or less at right angles to the longitudinal axis of that of the latter. In this position it would be exposed to the full force of the peristaltic motion of the body fluid of the moth larva, and being washed backwards and forwards would probably cause a good deal of interference with the general well-being of the host, whereas if orientated in the longitudinal axis with the help of the tail, it would offer relatively little resistance to this motion, and would itself be enabled to live a more comfortable existence. The consideration of the function of the tail brings forward the question—why is the head so heavily chitinized, and why has it such a long narrow shape ? As already pointed out, the high development of the cephalic skeleton, which does not seem to have any value to a larva living in a more or less passive manner, appears to be related to its use in effecting eclosion from the egg, and similarly it would seem that the shape and chitinization of the head is related to the form and size of the cephalic skeleton, and so to this same act of eclosion.

3. The method of respiration in endoparasitic larvae presents some difficulties. It is generally agreed that the earlier stages obtain oxygen from the blood of the host by a process of diffusion ; this diffusion being rendered possible because the partial pressure of dissolved oxygen in the latter is much higher than it is in the blood of the parasite. In the first-stage larva of *Glypta* there is no trace of a tracheal system, so that gaseous exchange of oxygen and carbon dioxide between the host and the parasite, or simple cutaneous respiration, appears to be sufficient to meet its needs. As it grows, however, a new system, or at least in the second and third stages an addition to the existing system, is required. In the second instar larva, tracheal trunks and transverse branches filled with some sort of gas make their appearance, and these in the succeeding stage are more developed, but in both instars the system is apneustic. The fourth and last stage, which does not live in a fluid medium, respires in the same way as an ectoparasite, that is by a peripneustic respiratory system with spiracles open to the external air. In both the first and the last instars the method of respiration is perfectly straightforward and requires no explanation, but in the intervening two instars the full story of the working of the tracheal system is not so apparent. In the first place we have to decide what is the nature of the gas which is contained in the tracheae. Obviously it must be either oxygen or carbon dioxide, or perhaps a mixture of both. It is a well-known fact that the carbon dioxide output of an insect is normally less than the oxygen intake, from which it can be deduced that there would be less carbon dioxide in the tissues and tracheae of these two stages than oxygen. Furthermore, carbon dioxide diffuses out of animal tissues thirty-five times more rapidly than oxygen, so that to appear in the form of a gas in the tracheae it would need to be present in the insect's tissues and blood in a very great amount, and in a very much higher concentration than oxygen. From a consideration of these two facts, we may safely assume that the gas in the tracheae of the second and third instar larvae of *G. haesitator* is not carbon dioxide but mostly oxygen. This oxygen must have entered through the walls of the tracheae, which are permeable to gases throughout their length, by a process of diffusion from the blood of the parasite larva, which in turn received it from the blood of the host in the same way. When it has been used up in the metabolic processes, this gas is transformed into carbon dioxide, which, because of its rapid rate of diffusion, should be able to escape directly from the tissues through the cuticle of the larva into the blood of the host, and so to the exterior. A point which is worthy of mention in connection with the filling of these tracheae with gas, is the possibility that they were initially filled with fluid. This has not been demonstrated in this species because of lack of opportunity, but the researches of Wigglesworth, Keilin, etc., on mosquito and other aquatic larvae, would appear to indicate that the apneustic tracheal system of these endoparasites,

just after ecdysis, may be filled with fluid.* If this is the case one wonders how the oxygen, at the low tension in which it is present in the parasite's blood, manages to force its way into the tracheae. Keilin attributed its entry to protoplasmic imbibition, a force exerted by the protoplasm of the cells, which causes the fluid to be absorbed out of the tubes so that a vacuum, into which the gases from the insect's blood diffuse readily, is left behind. According to Wigglesworth imbibition cannot account for the removal of the liquid, as this force would affect only the fluid in the immediate vicinity of the system concerned, and he suggests that it is absorbed by the process of osmosis. The extra activity at the time of ecdysis liberates certain metabolites in the tissues, and these products by increasing the osmotic pressure cause the fluid to be absorbed more rapidly.

Ascogaster quadridentatus, Wesm.

This species was found to be the commonest parasite of the pea moth in S.E. England. It was present in all the areas examined, the attack varying from 7 to 48 per cent. The highest figure (48 per cent.) was obtained in two areas, one in Bedfordshire, the other in Essex.

Percentage Attack in S.E. England.

TABLE II.

Year	Area	Parasitism per cent.
1935	Graveley, Cambridgeshire	20
,,	Huntingdon	16
,,	Wisbech, Cambridgeshire	10
1936	Honeydon, Bedfordshire	48
,,	Essex, 2	48
,,	Emneth, Cambridgeshire	40
,,	Gt. Shelford, Cambridgeshire	40
,,	Essex, 1	40
,,	Suffolk	36
,,	S. Lincoln, 2	36
,,	S. Lincoln, 1	20
,,	Farnham Royal, Buckinghamshire	6·6
1937	Essex, 3	45
,,	Marks Tey, Essex	40
,,	Essex 1	25
,,	Threekingham, S. Lincoln	12
,,	Essex, 2	10

Systematic Position, Host Records and Distribution.

Ascogaster quadridentatus belongs to the family BRACONIDAE, subfam. CHELONINAE. Its synonyms are as follows: *Ascogaster quadridens*, Herrich-Schäffer, *A. similis*, Ratz., and *A. bisulcatus*, H.-Schäffer. *A. carpocapsae* which has been reared from the codling moth in America and elsewhere has also been regarded as being taxonomically equivalent to *A. quadridentatus*, but Mr. H. R. Boyce, of Belleville, Canada, has some evidence to show that the two species are distinct. When he attempted to interbreed *carpocapsae* reared from the oriental fruit moth with *quadridentatus* from the pea moth, he found that copulation was vigorously resisted by the females. In addition to this seeming physiological incompatability a close examination of the adults revealed the presence of certain morphological

* Keilin & Thompson found that the tracheae were actually filled with fluid in certain Pipunculid larvae parasitic on *Typhlocyba* (Homoptera) (C. R. Soc. Biol., **78,** 1915, p. 9).

differences, especially in colour. He found that *carpocapsae* had the entire front tibiae, the bases of the middle and hind tibiae, and the trochanters of all the legs dark brown to brownish yellow; whereas in *quadridentatus* the legs had no light coloration, except for the entire front tibiae.

According to Szépligeti the special characteristics of the subfamily CHELONINAE are as follows: Abdomen broadly sessile, elliptical sutures absent. Wing with three cubital cells, radial cell short. The genus *Ascogaster* can easily be recognized by the sutureless dorsum of the abdomen (fig. 2, *b*). It differs from *Chelonus*, the only other genus with which it is likely to be confused, by the absence of hair on the eyes, and by the distinctly separate cubital and first discoidal cells of the forewing (in *Chelonus* these two cells are confluent). *A. quadridentatus* itself can be separated from the other species of *Ascogaster* by the black trochanters, and the presence of four strong teeth on the metathorax.

In the parasite catalogue of the Laboratory, sixty hosts are recorded for various species of *Ascogaster*. These are practically all Micro-Lepidoptera, and about three-quarters of them belong to the TORTRICOIDEA, the chief genera concerned being *Cydia*, *Tortrix*, and *Argyroploce*. *Ascogaster quadridentatus* itself has been recorded from the following: *Argyroploce variegana*, Hb., *Argyrotoxa bergmanniana*, L., *Clysia ambiguella*, Hb., *Cydia funebrana*, Tr., *Cydia molesta*, Busck, *Cydia pomonella*, L., *Cydia splendana*, Hb., *Eucosma ocellana*, F., *E. solandriana*, L., *E. tripunctana*, F., *Eupithecia absinthiata*, Clerck, *Hyponomeuta malinellus*, Zell., *Hyponomeuta padellus*, L., *Laverna hellerella*, Dup., *Pandemis heperana*, Schiff., *Polychrosis botrana*, Schiff., *Recurvaria nanella*, Hb., *Spilonota ocellana*, F., and *Tortrix* (*Cacoecia*) *rosana*, L. The distribution records associated with these species include Britain, France, Germany, Austria, Poland, Italy, the Crimea and the United States of America. From these records it will be seen that *Ascogaster quadridentatus* is a common parasite with a big host range and a wide distribution.

General Bionomics.

A good account of the life-history of this parasite and a general description of the primary larva has already been published by Rosenberg in his work on the codling moth (*Cydia pomonella*). Because of this it will be unnecessary for me to give a detailed description of the earlier stages, and a short recapitulation of the biology as observed on, and adapted to, the pea moth, will suffice. In addition to this, a certain amount of new work on the later instars, which is important from the point of view of morphology and identification and which was not covered by Rosenberg in his paper, is also included.

The adult parasite emerges from the host cocoon, in which it has overwintered, towards the end of June. Mating takes place soon after emergence and the females proceed to look for pea moth eggs in which to oviposit. The egg of the parasite (fig. 9, *a*) is deposited in the cytoplasm of the host egg, and after an incubation period of from two to three days, the newly emerged larva enters the embryo of the host and thus accompanies the latter when it enters the pea pod. Its development within the moth larva is very slow, so slow indeed that the latter has reached maturity and spun its cocoon while the parasite is still in the first stadium. In this stage it passes the winter. Early in the following summer it develops more rapidly and passes through two further larval stages, changes to a prepupa, then a pupa, and the imago emerging towards the end of June completes the life-cycle. In the laboratory the adult parasite lived for a period of from three weeks to a month.

Developmental Stages.

There are three larval stages, the first (fig. 9, *b*) and second being characterised by the anal vesicle, which is so typical of many Braconid larvae. This structure has arisen as an evagination of the proctodaeum and no really satisfactory explanation

of its function has yet been put forward. It has often been called a respiratory organ, but Thorpe (1932) concludes that though it may be of some use for respiration it is not the most important organ for the performance of this function, since even at its greatest development " gaseous exchange is taking place at a rate little if at all faster than that at the greater part of the body surface." Rosenberg suggested that since the fully grown first-stage larva is 250 times greater in volume than the newly hatched one, and the anal vesicle occupies one-sixth of the volume of the former,

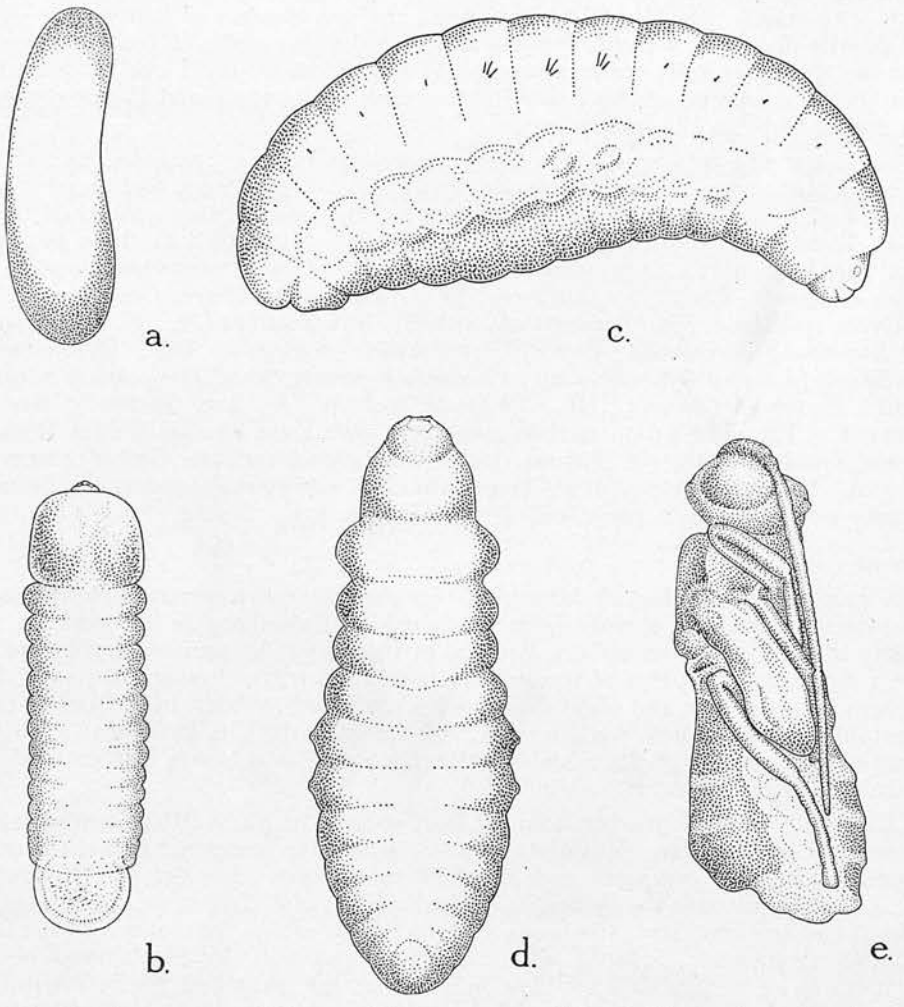

Fig. 9. *Ascogaster quadridentatus*, Wsm. ; *a*, egg (× 250) ; *b*, 1st stage larva (× about 33) ; *c*, mature larva (× about 14) ; *d*, prepupa (× about 14); *e*, pupa (× about 14).

its emission enables the larva to grow to such a degree in one stage. There is probably some truth in this suggestion, but it is doubtful if this is the whole story. Another characteristic feature of the first stage larva is the tremendous development of the first body segment which contains the cerebral ganglia. Compared with it the head, which has not altered in size, looks small and insignificant. The mature larva (fig. 9,·*c*) is yellowish white in colour and measures about 0·6 mm. in length by 1·8 mm. in maximum breadth. A peculiar characteristic is the enlarged abdominal region

which is much broader than the head and anterior segments. On the pleurae of segments 6 and 7 a pair of large pointed papillate lobes are present, and the last segment, when viewed from behind, has the appearance of a figure 8. In this instar the anal vesicle is absent, but other structures, notably the cephalic skeleton, spiracles and skin armature, afford very useful clues to identification.

The cephalic skeleton (fig. 6, *c*) is noteworthy chiefly on account of the mandibles, which are narrow, elongated and toothed. This latter characteristic enables one to distinguish the larva of the Braconid, *Ascogaster*, from the larvae of the two Ichneumonid parasites of the pea moth. The superior and inferior mandibular struts with the connecting pleurostoma are present, but there is no trace of an epistoma, and the hypostoma is unchitinized. The labial ring is rather quadrangular in outline and is broken at the top in the region of the silk-duct opening. On either side of it there is a well developed labial strut. The non-chitinized areas are the clypeus, with two pairs of setae, the labrum and the maxillae, each of the latter with a sensilla, which with the pair of similar sensillae on the labium are regarded as being analogous to the maxillary and labial palps. A large number of setae are distributed over the region of the cephalic skeleton, chiefly in the labial and sub-labial areas and at the base of the maxillae. The antennae are represented by a pair of circular chitinized areas on the dorsal surface of the head, each containing two small papillae.

The respiratory system consists of a pair of longitudinal tracheal trunks with transverse commissures in segments 2 and 11, and transverse branches emitted from the junction of the spiracular tracheae with the longitudinal trunk in the anterior margin of the segments. There is no accessory system in the thoracic region such as is usually found in the ICHNEUMONIDAE. Altogether there are seven pairs of spiracles in segments 2 and 4–9, and the system is peripneustic. The thoracic and abdominal spiracles (fig. 7, *e*) are similar in shape and construction, but the former are somewhat larger. They consist of an oval atrium, followed by a tube composed of a varying number (16–23) of chitinized rings, and this in turn leads on to a valvular apparatus made up of two elongated ovoidal bodies with a narrow channel between them. From this closing apparatus, a short length of trachea joins the spiracle to the longitudinal trunk. The measurements of the atrium are as follows :—

TABLE III.

	Thoracic spiracle	Abdominal
Diameter	32–36 μ	25–31 μ
Depth	19 μ	17–18 μ
Diam. of opening ...	14 μ	10–14 μ

One of the most characteristic features of this larva is the rather striking and unusual skin armature (fig. 7, *a*, *b*). It consists of a close general covering of small pointed setae which are roughly triangular in shape and measure about 7 μ across at the base and about 4 μ in height, in which are interspersed dorsally at fairly wide intervals short solitary spines 18 μ in length. In addition to the latter a third set of very large spines 64–72 μ in length are to be found on the dorsal surface of segments 5–7, two groups of three to four spines being present on each of these segments.

The cocoon (fig. 8, *b*), which is constructed of very thin hyaline parchment-like material, can easily be distinguished from the cocoons of the other parasites of the pea moth by the broad whitish median band formed from circularly wound fibres. It measures 6 mm. in length by 2·5 mm. in breadth ; the circular band is about 1·7 mm. in breadth.

The prepupa (fig. 9, *d*), which measures 5·46 mm. in length by 1·95 mm. in maximum breadth, is differentiated into three distinct regions—the head, consisting

of the old larval head and the broad quadrate first body segment now showing the rudiments of the imaginal eye ; the thorax, formed from segments 2–4 ; and the somewhat ovate abdomen, made up of the nine remaining segments. As in the mature larvae, on the second and third abdominal segments there is a pair of lateral papillate lobes, and the terminal segment is curved ventrally and is somewhat obliquely truncated. In colour the prepupa is yellowish and shiny, and the skin is shagreened with small tubercles, the large spines mentioned in connection with the mature larva being visible on the first and third abdominal segments.

When newly formed the pupa (fig. 9, *e*) is yellowish white in colour with dark brown eyes and ocelli. As it gets older the dorsal surface changes to a shiny jet black. Ventrally it is black except for the hyaline antennae, palpi, wings and greater part of the legs. The abdomen is very characteristic. It consists of a small black dorsal carapace, formed by the fusion of the tegmina, perched on top of the soft, yellow and greatly distended venter. On the latter there are four black plates separated by yellow tissue. As the pupa nears maturity this swollen region of the abdomen contracts, and the lower median plates come to lie underneath the sutureless dorsum. The duration of the pupal stage at 26°C. and R.H. 60 per cent. is seven days. Length of pupa 4·7 mm., maximum breadth 1·4 mm.

Angitia sp. (near **rufipes,** Grav.).

This parasite was submitted to Dr. Ferriére of the Imperial Institute of Entomology and identified as a member of the genus *Angitia*, a genus in which the species are very numerous and difficult to separate. As it differed from the named specimens in the collection, and because the members of this group have not yet been properly worked out and classified, he was unable to give it a specific name. It seems quite possible that this is a new species. In Schmiedeknecht's key it runs to *A. claripennis*, but Dr. Ferrière thinks that it is more closely related to the succeeding species, *A. rufipes*, Grav. It differs from the latter mainly by the coloration of the hind tibiae, which are dark at the base and top and yellowish in the middle, whereas they are almost quite red in *rufipes*. As a parasite of the pea moth it was comparatively rare, occurring in only about 2 per cent. of the larvae. The material from which it emerged was collected in Cambridgeshire and Essex.

Systematic Position, Host Records and Distribution.

Family ICHNEUMONIDAE ; subfamily OPHIONINAE ; tribe CAMPOPLEGINI. According to Schmiedeknecht the CAMPOPLEGINI can be recognised by the following characters—recurrent nerve emitted behind the areolar nerve ; middle tibiae with two spurs ; thorax smooth ; hind tarsi not thickened ; stigma long and narrow, radial cell drawn out ; abdomen (fig. 2, *c*) petiolate ; spiracles mostly round and situated behind the middle of the first segment ; notauli scarcely marked. The genus *Angitia* itself can be distinguished by the nervellus of the hind wing, which is mostly vertical and never geniculate, and by the petiolar area of the propodeon, which is only slightly excavated.

Developmental Stages.

On account of the comparative rarity of this species it was difficult to obtain material for a description of the developmental stages. Nevertheless, all the important instars except the egg are adequately described in the following pages.

The primary larva (fig. 10, *a*), which consists of a head and thirteen body segments, is more or less translucent, except for the brown, strongly chitinized head. It is of the usual internal ichneumoniform shape, already described in the case of *Glypta haesitator*. An extremely interesting character of the larva is the presence of paired protopods on each of segments 1–12, the last seven or eight pairs of which are about 0·021 mm. in length and somewhat longer than the anterior ones. In contrast to

Glypta, a fairly well-defined tracheal system, consisting of two longitudinal trunks with lateral branches in segments 1–12, two accessory trunks in the thoracic region, and extensions to the head and tail, is present. Situated on the dorsal surface of the head there is a pair of grooves, which, beginning at the posterior end become narrowed anteriorly until they stop short near the front margin. Similar grooves have been described by Thompson and Parker in the first stage larva of *Eulimneria crassifemur* and by Thorpe in *Eulimneria rufifemur*, *Omorgus mutabilis* and *Cremastus interruptor*, the first three, like *Angitia*, being members of the CAMPOPLEGINI and all of them Ophionines. Besides these grooves, the head is characterised by a pair of posterior ventral lobes, a small posterior dorsal lobe with a slight groove, a number of sensoria

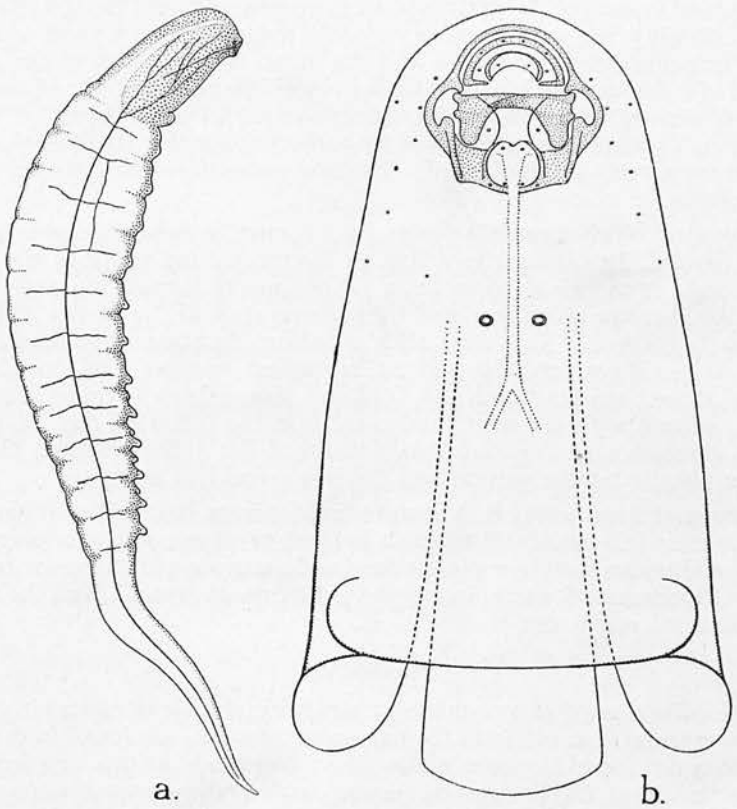

Fig. 10. *Angitia* sp. : *a*, 1st stage larva (note protopods and dorsal grooves on head) (× 50) ; *b*, ventral view of head showing cephalic skeleton (× 300).

in and around the cephalic skeleton region, and a pair of small antennae. The cephalic skeleton (fig. 10, *b*) is similar in general outline and appearance to that of *Glypta haesitator*, except that it is much larger. A detailed description will therefore be unnecessary as the names of the various parts can be obtained by reference to fig. 4.

The full-grown first-stage larva measures 2·08 mm. in length by 0·26 mm. in maximum breadth, the length of the head being 0·325 mm., and the length of the tail 0·715 mm.

The drawings and description of the cephalic skeleton, skin armature and spiracles of the last instar have been made from a mount of the cast skin. Although constructed

on the same general plan, the cephalic skeleton of this species (fig. 6, *b*) is quite distinct from that of *Glypta haesitator*. The main differences are in the labial and maxillary areas, and in the mandibles, which are smaller than those of *Glypta* (0·09 mm. in length compared with 0·12 mm.). Probably the most striking difference is to be found in the labial area, where the labial ring broadens out at the bottom and where a Y-shaped chitinized area is present below the opening of the silk duct. The maxillary strut is also rather short and thick, compared with the more elongated one of *Glypta*, and the hypostomal arms, although rather broad and well-developed, do not curve round the labial area so much as in the latter species. The labial strut is also much shorter and the arrangement of the setae is different, but all these points can be better appreciated by comparing the actual drawings in fig. 6.

The tracheal system of the mature larva is peripneustic and the spiracles are very small and difficult to see, except under very high magnification, a point which affords a ready distinction between *Angitia* and the other two parasites of the pea moth, *Glypta* and *Ascogaster*, which have relatively huge spiracles (fig. 7). A more or less oval-shaped atrium, with an average diameter of 14 μ, a depth of 10 μ, and an opening of 7 μ diameter, is followed by a short spiracular trachea, the structure of which is very weak and ill-defined. The skin armature closely resembles that of *Glypta haesitator*.

The prepupa, which measures 6 mm. by 1·8 mm., is somewhat similar in shape to that of *Glypta*. In colour it is yellow on the thorax and white on the abdomen. This stage lasts from two to three days. When newly formed the pupa is whitish in colour, the eyes are prominent and the segmentation of the thorax and abdomen is very clearly marked. Nine days after pupating (duration of pupal stage during cold spell sixteen days, probably shorter in warmer weather) the thorax begins to darken and three days later both the head and thorax become quite black, making a striking contrast with the white abdomen. On the following day, or three days before the emergence of the adult, the dorsum of the abdomen turns black, while the swollen pleurae remain yellow, and the wings and legs are grey.

The cocoon of *Angitia* (fig. 8, *c*) is quite distinct from that of the other parasites of the pea moth. It is mainly dark brown to black in colour, with a number of loosely woven white fibres scattered over its surface, and a narrow white circular band round its centre. It measures 5·4 mm. in length by 1·8 mm. in breadth, and the breadth of the circular band is 0·5 mm.

Nematodes.

A small collection of larvae made at Graveley, Cambridgeshire, in September 1936 and overwintered in soil from the Laboratory garden, was found in the following spring to have developed a severe infestation of Nematode worms. In fact so heavy was the attack that all the resting larvae within the cocoons were eventually destroyed by these parasites. Preserved specimens were submitted to Dr. H. A. Baylis, the Nematode expert at the British Museum, and he replied as follows " . . . . . I am unable to identify these worms and I suspect they are something new. But in many ways they resemble *Neoaplectana glaseri*, Steiner (1932), a parasite of *Popillia japonica*. I do not think they are congeneric but there are considerable resemblances, not only in morphology but apparently also in habits and life-history." He goes on to say that before its identity can be established a considerable amount of time would be required in order to work out the life-history so that one could make sure all the various forms are really stages of the same species. Unfortunately it has been found impossible for the writer to devote the necessary time to the rearing of this worm, so that its exact identity must, at present, remain undisclosed. In connection with its possible value for biological control purposes reference may be made to the work of Glaser on *Neoaplectana*. The latter was found by this worker in a limited area in New Jersey, when during the years 1929 to 1931

it caused a high mortality amongst the larvae of the Japanese beetle (*Popillia japonica*). After a time Glaser was able to rear the worm on two kinds of artificial media, one consisting of dextrose-veal-infusion agar with desiccated cow's ovaries, and the other of Irish and sweet potatoes, etc. He found that there were four stages in the life-history, the second being the infective one. Entry into the host was gained via the mouth and two or three generations of nemas were developed within the host's body before all the tissues of the latter were consumed. In trying to introduce the parasite into areas where it was absent, Glaser sprinkled the soil with water containing the invasive form, but this method proved unsuccessful. Later on he buried the cultures in holes in the ground and claimed that as a result of this introduction the grub population in the treated area, when compared with the numbers in the surrounding untreated area, was considerably reduced. He concludes his paper by saying that other factors such as birds, moles, climate, etc., affect the population of the grubs, so that it is impossible to maintain a constant heavy population of the worm over a period of years within a given territory.

The work done by Glaser and others in this field is fairly recent, so that it is not yet possible to make a definite statement on the value of Nematode worms for the purpose of biological control.

Fungi.

At various times overwintering larvae were found which had succumbed to the attack of fungi. These were submitted to Mr. T. Petch, the specialist on entomophagous fungi, who isolated and identified the following three species: *Beauveria bassiana*, *Isaria farinosa*, and *Gymnoascus ruber*. The last named he considered to be secondary, following on the attack of the other two. The second—*Isaria farinosa*—developed into a rather peculiar form of this species, the reproductive apparatus taking the form of stalked inflated clubs (Plate VIII, fig. 2) similar to some Mr. Petch had seen before on Coleoptera from North America. In the containers in which the cocoons were stored in the laboratory the percentage attack by fungi varied with the amount of moisture. Usually it was low, because the soil was kept in the right condition, but if at any time the moisture present exceeded the optimum, mortality from this factor was very considerably increased. No attempt was made to estimate the percentage mortality due to fungus attack in the field, because of the difficulty of locating cocoons, but it is probable that the death rate from this cause is quite appreciable.

Thus far, although some slight successes have been obtained from their use, entomophagous fungi have proved of little value in the control of injurious insects. This is chiefly due to the fact that the following three conditions—a warm, humid atmosphere and a crowded condition of the host population, must usually be fulfilled before an outbreak can occur. When these conditions are not satisfied it is very unlikely that the introduction of fungi, either directly or from cultures on artificial media, will result in an induced outbreak with a definite control value.

The Influence of Climatic Factors.

Although an extensive study of the effect of climatic factors on the population of the pea moth was quite impossible during the course of the present investigation, a few observations on this subject were made, which may be of some importance. In the first place, it will be necessary to consider the factors which influence the distribution of the pea crop itself, for the distribution and abundance of the moth is obviously intimately associated with that of its host. According to a well-known agricultural authority, peas are more susceptible to wet weather than cereals, and the factors chiefly affecting their distribution are the amount of sunshine and summer rainfall. Because of this their cultivation is confined to the drier and sunnier eastern and south-eastern counties of England, from the East Riding of Yorkshire in the north, to Sussex and Surrey in the south, Worcester in the west being the only notable

exception. The proportion of peas to cereals is said to be greatest in Kent, Essex, Suffolk and Lincolnshire. My own experience, confirmed by various pea salesmen, leads me to suggest that the chief pea-producing counties are Essex for the earlier lots, and Lincoln and Yorkshire for the later supplies. London's huge vegetable markets are supplied with peas mainly from these counties. Large quantities are also grown in Huntingdon, Cambridgeshire, Bedfordshire and Suffolk, but a big proportion of these, along with some from south Lincoln, go to the canneries situated in the region of the Wash at Wisbech, King's Lynn, Huntingdon, etc., while the western markets and canneries obtain their stocks from the Worcester area. Apart from climate, the edaphic or soil factor is of importance, a light calcareous loam being the best soil for pea cultivation. Such a soil is found in parts of Essex, and certain other pea-growing districts, and the combination of suitable soil and climate makes this county a more or less ideal place for the growing of large quantities of peas.

In these eastern counties one would expect to find the pea moth fairly evenly distributed, but this is not the case. Although the supply of host material is abundant in each of them, only in Essex and the counties up to south Lincoln was it found in worth-while numbers. On the farms in north Lincoln no trace of it was discovered, and in Yorkshire it appears to be an equally rare insect. It is true that a few specimens were obtained from gardens on the Yorkshire coast, but field crops were usually unaffected. This conclusion was confirmed by market salesmen who handle large consignments from both Yorkshire and Essex. The Yorkshire product is nearly always " clean," but in comparison Essex peas, although not really very heavily attacked, are almost a byword. From a consideration of the situation it would appear that certain climatic factors operate on the moth at one or more stages in its life-history, so that its range is limited to suitable habitats. What these factors may be has not yet been definitely determined, but the following suggestions may be considered. Probably moisture either in the form of rain, or when present in excess in the soil, is one of the most important controlling factors. Excess moisture would affect three stages of the insect—the cocoon, the adult, and the newly hatched larva. In a damp moist winter with a high rainfall, and especially in a retentive soil, a high mortality from fungus attack in the cocoon stage would be expected. Again, a wet July and August would be reflected in greatly reduced numbers of moths in the following year, because the insect loves bright sunshine, and wet weather at the time of oviposition would considerably curtail the egg-laying activities of the female. It is also possible that the newly hatched larvae, when wandering around on the surface of the pods before tunnelling inside get washed off by any heavy rainfall which occurs during these two months. A comparison of the rainfall figures over a long period of years for Yorkshire, where the moth is practically unknown, and Essex, where it is moderately common, is interesting.

TABLE IV.

Locality	Average yearly rainfall	Rainfall in cocoon months (Sept.–June, inc.)	Rainfall in moth and early larva months (July-August)
Brigg, N. Linc. ...	25·38 in.	20·27 in.	5·11 in.
Hull, S. York	25·38 in.	20·13 in.	5·25 in.
Clacton, Essex	19·26 in.	15·43 in.	3·83 in.
Chelmsford, Essex ...	22·49 in.	18·15 in.	4·34 in.
Average :			
York.–N. Linc.	25·38 in.	20·20 in.	5·18 in.
Essex	20·88 in.	16·80 in.	4·08 in.
Difference	4·5 in.	3·4 in.	1·1 in.

It will be seen from this table that the difference in rainfall between the two areas, both at the time when the moth is in the cocoon stage and when it is in the adult and early larval stages, is quite appreciable, and the heavier rainfall may partly account for the absence of the insect from the northern counties.

The moth's love of bright sunshine has been noted on several occasions, and by several observers, so that a comparison of the sunshine figures for Essex and Yorkshire will also be interesting:—

TABLE V.

Locality	No. of hours sunshine in June–August
Hull, Yorks	554 hours
Clacton, Essex ...	639 hours
Difference	85 hours

The temperature during these months is considerably higher in Essex than in Yorkshire and this may also be important, but further figures are unnecessary. In the accompanying maps (fig. 11) the differences in the amounts of rainfall and sunshine are more clearly brought out.

To sum up, it would appear from the available data that the climatic requirements of the pea moth in England are, a hot, dry, sunny summer, and a fairly low rainfall during the winter and early summer months.

4. Notes on Cultural and Chemical Methods of Control.

A brief record of the attempts which have been made to control the pea moth by cultural and chemical methods may be introduced here. The inadequacy of these modes of attack, especially of the latter, will clearly demonstrate the necessity that exists for the trial of natural methods of control such as are advocated in this paper.

The best cultural aids as recommended by various authorities are :

1. Early maturing varieties of peas should be selected and sown as soon as possible so that the crop may be well advanced before egg-laying by the moth becomes general. In Cambridgeshire (Min. Agric. Rept. Path. Lab., Oct. 1927), the percentage attack on *Gradus* peas sown on the 8th and 22nd April, 1927, was only half that on those sown on 6th May. Mid-season and later varieties are said to be more susceptible to attack.

2. When a bad infestation is known to exist the peas should be picked green in order to prevent as many as possible of the larvae from entering the soil to pupate.

3. Disking of the soil after the crop is harvested will kill some of the overwintering forms. Deep ploughing in order to bury the cocoons has also been suggested as a control measure, but since (according to Hanson and Webster) the larvae, when deeply buried, leave their cocoons and seek pupation sites below the surface of the soil, this method would not seem to be of much value.

4. Poultry should be run on the land when it is being cultivated, so that they may eat as many cocoons as possible.

5. In order to get rid of the larvae which still remain in the pods after the crop has been removed from the field, threshing should be carried out within a day or two of harvesting and the resulting straw, together with any vines that have been left in the fields, should be gathered up and burned.

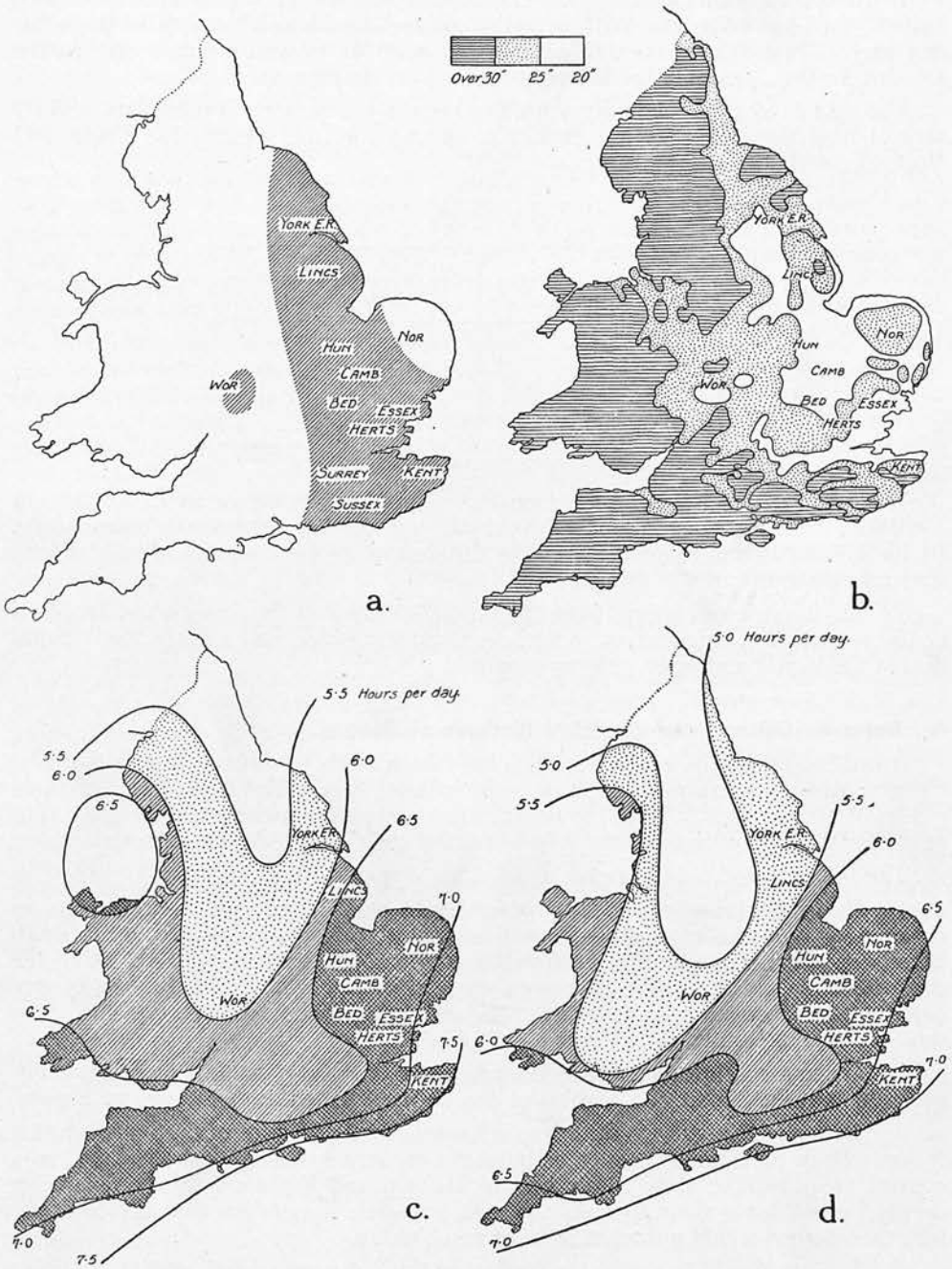

Fig. 11. Maps of England showing : *a*, main pea-growing counties ; *b*, average annual rainfall ; *c* and *d*, normal distribution of sunshine during July and August. (*b*, from Rainfall Atlas, *c* and *d*, from Air Ministry's Book of Normals of Meteorological Elements, by permission of the Controller of H.M. Stationery Office and the Council of the Royal Meteorological Society.)

Little or no success appears to have attended attempts at spraying with chemicals, and this method of control is regarded (Fluke) as an impracticable proposition for the following reasons :—firstly, because at the time when the eggs are hatching the pea vines fall over and become matted together, so that it is impossible to get a good coating of poison on all sides of the pod ; secondly, because new pods develop so rapidly that several closely repeated sprayings are necessary to be really effective ; thirdly, because the foliage, when coated with so much poison, is of doubtful value for feeding to stock ; and fourthly, because a great deal of damage is done to the crop by driving through it in the course of spraying operations.

Actual tests of various chemicals both in dust and liquid form have been tried in this country and in Canada. In England, Miles (1926) tried derris extract, soap and nicotine, lead arsenate and a number of other preparations, but the results which he obtained do not indicate that any of these chemicals are of much real value for the control of the moth. Several arsenical compounds were also tested by Brittain in Canada, but in dust form he found they had practically no effect, whilst the only liquid which appeared to have any value at all (and this rather doubtful and uncertain) was calcium arsenate.

5. Collection, Sorting and Shipment of Material.

Various methods of collecting moth-infested peas were tried, and different sources of supply exploited at the beginning of the investigation, but after a time all except three, which gave eminently satisfactory results, were discarded. These three consisted in the examination of pea stocks (*a*) at canning factories, (*b*) in the field, in areas where the moth was known to be present, and (*c*) at Covent Garden vegetable market in London. The leading canneries in the Huntingdon, Wisbech, and Kings Lynn districts, which handled pods in sacks, were visited from time to time during the pea-packing season, and the stocks on hand were examined for moth-infested material. This initial sampling of material in sacks was supplemented by observation of the machine-shelled peas as they travelled slowly along on a conveyor belt between rows of women, who picked out moth-attacked and otherwise damaged peas to prevent their inclusion in the finished product. In the main crop supplies a small percentage of moth-attacked peas was nearly always to be found on the belt, but whenever this percentage appeared to be higher than usual the lot in process of manufacture was traced back to its source on the loading bank. Here samples were taken from the actual consignment in order to get the exact degree of infestation and the percentage of parasitism. Usually a few sacks of this material could be bought from the manager of the factory, but the main value of the examination lay in the location of an infested area which resulted. This led on to visiting various farms as described in the next method of collecting. Sometimes when a particularly bad lot of peas was handled by the cannery the whole consignment could be bought up at lower than market rates, but this did not happen often, as the percentage of attack in their supplies was usually quite low.

When a clue to an infested area was obtained at the cannery in the manner described in the preceding paragraph, a visit was paid to the farm in order to buy up as much of the crop as remained. If the farmer had sold all his peas to the factory, it was often found possible to find equally good material in the immediate neighbourhood. In addition to the farms visited as a result of information obtained at the canneries, a certain amount of free-lance searching was carried out in areas known to have a moderate yearly infestation of pea moth, such as the county of Essex, where good numbers of parasitized larvae were occasionally obtained.

The third successful method of collection consisted in visiting Covent Garden vegetable market very early in the morning before real activity in buying and selling commenced. Samples were taken from the various consignments on sale and the larvae dissected for parasites in the open market. When suitably infested and

parasitized material was discovered, bids were made for it through one of the salesmen. At first this method was not very satisfactory, as the dealers thought this was some sort of underhand dodge to test the purity of their stocks, but once they were convinced I was genuinely seeking for " maggoty peas " (as they called them) for research purposes, and was prepared to pay market prices for them, their attitude changed from one of distrust to one of distinct helpfulness, so that the market eventually proved to be one of my best sources of supply.

Since it was essential that the freshly gathered peas should not remain for any length of time in the sacks, because of the fermentation which would inevitably set up in the green pods and thus cause the death of the enclosed larvae, all material was promptly despatched by train and motor lorry to the laboratory. Immediately on arrival the sacks were emptied and the pods spread out thinly on the cool stone floors of the sorting rooms. They were then opened by a team of women who placed the infested peas in trays, and discarded the remainder. These trays were then handed over to a second group of workers who sorted out the larvae into two lots, one consisting of immature and the other of fully grown larvae. The latter were placed in slightly moist sterilised soil in large wooden trays 20 in. square by 3 in. deep with a copper gauze ventilation piece in the lid. In this soil they, in due course, spun their cocoons. The immature larvae were left to feed up in pods placed side by side on a zinc gauze tray within a wooden container (Plate VIII, fig. 1) similar to that used for the mature larvae. They were examined from time to time, given fresh food when necessary, and when fully grown were removed and treated in the same way as the earlier lots of mature larvae.

As a rule the peas were bought when the majority of the larvae had attained maturity, but if a young infestation was found in the field, instructions were left with the farmer to delay the picking of the crop until a certain date, by which time it was known that most of the larvae would be in the final stadium. Sometimes, however, an excellently parasitized consignment was received from the canneries in which the caterpillars were not more than half grown. In this case the pods were scattered over the sorting-room floor, and kept for a week or a fortnight before the procedure described in the preceding paragraph was brought into operation. The only attention necessary during this waiting period was an occasional shuffle and the removal of any decayed material. This method answered quite well if the pods were in good condition on arrival, but if picked when not quite dry or if kept too long in the sacks, large consignments would have very quickly decayed had they not been handled immediately.

Various accounts in the literature emphasize the extreme difficulty which collectors have experienced in rearing this moth through to the adult stage. The method which gave most satisfactory results at Farnham House Laboratory will therefore be of interest. First of all, it is necessary that the proper degree of humidity be maintained in the tins of soil in which the cocoons are hibernating. Failure to observe this important point is fatal, for if the soil becomes too dry the larvae soon shrivel up, and if too moist, various species of fungi find more or less ideal conditions and exact a heavy toll. Small tins (4 in. in diameter by 2 in. deep with a 1 in. diameter gauze ventilation hole in the lid) almost half full of slightly moist sterilised soil, were found to be the most useful containers for the cocoons. These were kept in an outdoor insectary and examined every Monday morning during the hibernating period. If it was found that the soil showed signs of drying out the cocoons were carefully sifted out with a minimum of disturbance and the old soil replaced by a fresh lot, which had been lightly, but thoroughly, moistened. Water was never added to the tins from above, as this tended to encourage the growth of fungi. Several other methods were also tested, but the one described was found to be the most satisfactory.

For shipment, the cocoons were removed from the trays in which they had spun up and placed in slightly moistened sterilised soil, in tin boxes 9 in. square by 5 in. deep. These boxes were then packed with excelsior in large wooden cases and despatched to Mr. Baird of the Parasite Laboratory at Belleville in Canada.

6. Prospects of Biological Control in Canada.

The problem is evidently suitable for the application of biological methods of control, because, as already stated, the pea moth is alien to Canada, and because a survey by the authorities has failed to reveal the presence of any parasites on the insect in the Dominion. Although the abundance of the moth is not necessarily altogether due to the absence of parasites, the facts seem to point that way, especially so if we compare the conditions obtaining in Canada with those in England—in the former country a high infestation level of the moth, and the absence of parasites, and in the latter a comparatively low infestation level with occasional spasmodic outbreaks, and a fairly high percentage of parasitic attack. In these respects the problem parallels other attempts at biological control. Furthermore, the failure of attempts to control the pest by the use of chemicals, and the limitation of cultural modes of suppression, leaves biological control as the only method which offers any hope of ultimate success.

Before proceeding further it may be as well to point out the many difficulties which confront one, when an attempt is made to express mathematically the amount of control exercised by the parasites of the pea moth on their host. In the first place peas are never grown in the same field for two years in succession, and the distance between one year's crop and the next may be as much as half a mile or more. As a result of this practice of crop rotation a migration of moths and parasites from one area to another takes place. During this migratory period factors of mortality may enter into the history of a population which are extremely difficult to evaluate. In addition to the probable loss of individuals on any particular farm from this cause, there is also the possibility of an influx of new moths and parasites from adjoining farms to consider. The increase in numbers of a population from such immigration would depend on the nearness of a crop to the field on the neighbouring farm where peas were grown the previous year. These two factors alone would so complicate the data as to render figures of moth infestation and parasitism for two or more successive years uncomparable, but there are still others to be taken into account. For example, the quantity of peas grown on a farm varies from year to year. If a farmer is offered a low price for his crop one year, he may grow a smaller area of peas in the following season, and if, on the other hand, high prices prevail he may increase the acreage. The question of varieties is also important, because some are more susceptible to attack than others, and the amount of any particular variety grown on a farm is never constant, but varies according to local conditions, the law of supply and demand, or even to a desire for trying new types or strains, etc. This variation in the amount and composition of the crop from one year to another must have an important effect not only on the relationship between the moth and its host, but also, as a necessary consequence, on that between the moth and its parasites. During the years 1936–37 figures of moth infestation and parasitism were obtained for two successive seasons from a number of farms (the areas from which infested peas were secured in 1937 were not always, or even often, the same as those in 1936, because for economic reasons the most heavily infested and parasitized material was selected as opportunity offered at canning factory or market), but when the importance of these complicating factors was realised, no attempt was made to correlate them. I think it has been clearly demonstrated that such correlation would be scientifically unsound, and any results obtained would almost certainly be misleading. In order to obtain a graphic representation of the influence which the parasites exercise on their host, it would be necessary to compile the true history of an infestation over an

extended period, and such a study could only be carried out if a crop of one variety of peas were grown on a large isolated field for several years in succession. With an expensive crop like peas this proceeding would be economically impossible, unless plenty of funds were available, and even then, a further difficulty would arise. In obtaining the necessary data, large samples of pods would have to be taken from the experimental field, opened up and any larvae found in them extracted and dissected for parasites. As a result these individuals, both moth larvae and parasites, would be lost to their respective populations, and not only they themselves, but their potential progeny as well, so that in the end, although fairly satisfactory results might be obtained, they would really only be approximate. It follows then from these remarks, that the study of biological control by the method of mathematical analysis in insect pests of field crops which, like peas, are subject to cultural and economic manipulation is rather a difficult proposition. More suitable for this type of research would be a pest of forest trees, or of weeds in a natural habitat, where the host-plant is not subject, or not unduly subject, to the limitations imposed by cultural activities.

So far then as the pea moth is concerned the most that one can say in regard to the probable effect of the introduction of parasites into Canada is that certain parasites have been found attacking the insect in England where its population is at a comparatively low level, and that in Canada where this moth is a serious pest, parasites are absent. In previous biological control projects the main evidence for the success of the work was the abundance of the pest prior to the introduction of parasites, and its comparative scarcity, or at least considerable reduction in numbers, after they had become established. We must employ the same method for the pea moth and wait hopefully to see what ultimate effect these parasites will have when they become plentiful in their new environment.

Before leaving the subject of control, we may briefly take note of the different species of parasites which are being, or will be, employed by the entomologists in charge of the Canadian end of the work.

The parasite complex on the pea moth in England, which has been fairly thoroughly investigated by the writer, consists of three species, *Ascogaster quadridentatus*. *Glypta haesitator* and *Angitia* sp. For the three together, the highest percentage of parasitism obtained in the course of the investigation was 60 per cent., and 45–50 per cent. might be taken as the average attack during the years 1936–37.

In addition to these three parasites which have been liberated in Canada, the Dominion entomologists are attempting to employ those from a closely allied species of moth (*Cydia molesta*) already present in that country. Some of these, including *Macrocentrus ancylivorus*, *M. thoracicus*, *Glypta rufiscutellaris*, *Microdus* (*Bassus*) *diversus* and *Ascogaster carpocapsae*, have proved quite effective against this latter pest and they can be bred in fair numbers under artificial conditions. Already consignments of *Macrocentrus ancylivorus* and *Ascogaster carpocapsae* bred from *C. molesta* have been liberated along with the imported English species in the infested areas. Whether they will attack the moth in the field without first being reared from it under artificial conditions remains to be seen, but it is interesting to note that both *Macrocentrus ancylivorus* and *M. thoracicus* have completed their life-cycle on the pea moth in the laboratory.

In conclusion, it is hoped that this combination of English and Canadian parasites may prove so formidable, that it will eventually reduce the numbers of the pea moth to a point where a greatly increased margin of profit will become available for the growers who have suffered so severely from the depredations of this undesirable pest.

7. Summary.

1. The moth—*Cydia nigricana*—whose larvae bore into the pods of developing peas and render most of the contained seeds unfit for human consumption is

considered by some authorities to be one of the principal insect pests of agriculture in Canada. It is particularly destructive in the Maritime Provinces and British Columbia, while in Ontario it increased to such proportions that the farmers of that province had to give up growing mid-season peas altogether.

2. This state of affairs is attributed to the fact that the pea moth was accidentally introduced from Europe in 1893 without the insect parasites which attack and check it in its native home. At any rate no parasites have emerged from the representative collections of pea moth material made by the Canadian entomologists in the affected areas, while three species with a combined parasitism of up to 60 per cent. have been reared by the writer from cocoons of the moth in England. Furthermore, in Canada, where parasites of this particular pest are absent, 10–50 per cent. of the pea crop and sometimes as much as 75 per cent. or more, is said to be destroyed annually by the moth larvae, whereas in England, where they are present, the attack is usually comparatively slight.

3. The paper opens with a general account of the biology of the pea moth including systematic descriptions of the adult and developmental stages, and notes on the host-plants and distribution of the insect.

4. Three species of internal parasites: *Ascogaster quadridentatus* (Braconid), *Glypta haesitator* (Ichneumonid) and *Angitia* sp. (nr. *rufipes*) (Ichneumonid), the first of which oviposits in the egg and the other two in the larvae of the host, were reared from the cocoons of the moth. Keys to the adult and developmental stages of these parasites have been drawn up, and a fairly full account of their biology, host records, and distribution, together with a detailed study of the developmental stages, has been prepared.

5. The developmental stages of the Ichneumonid, *Glypta haesitator*, which possess some interesting features, have been given special attention and the significance of certain structures such as the cephalic skeleton, the elongated head and tail, and the respiratory system, is discussed.

6. Some of the cocoons were found to contain a large number of nematode worms, which had destroyed the hibernating larvae. These were submitted to a specialist who unfortunately was unable to identify them, and who thought they were in all probability something new. It is possible that they are nearly related to *Neoaplectana glaseri*, a worm which attacks the Japanese beetle, *Popillia japonica*. The work of Glaser on *Neoaplectana* and its relation to natural control is reviewed.

7. Three species of fungi, *Beauveria bassiana*, *Isaria farinosa* and *Gymnoascus ruber*, have been isolated from the cocoons. The last named species is thought to be secondary following on the attack of the others. *Isaria farinosa* appears in a special and interesting form on this host.

8. Because of its climatic requirements the pea crop is grown mainly in the S.E. counties of England from the East Riding of York to Surrey. Within this pea-growing area the insect was found to be more common in Essex, parts of Cambridgeshire, Huntingdon, and S. Lincoln, etc., whereas in N. Lincoln and Yorkshire it was conspicuous only by its absence. The apparent significance of rainfall, sunshine and temperature on this distribution is discussed.

9. Cultural methods of control may be of some slight value, but chemicals, because of (*a*) the inacessibility of the larva, (*b*) the difficulty of wetting the pod all round in order to trap the newly hatched larva, (*c*) the need for almost continuous spraying with the daily development of new pods, (*d*) the danger to stock of accumulated poison on the pods and foliage, and (*e*) the damage caused to the crop by driving through it with spraying machines, have entirely failed. Biological control is therefore the only method which remains to be tried, and it is also the only one which offers any hope of success.

10. A description of the methods employed in collecting, sorting, and shipping material, followed by a short discussion on the prospects of the ultimate control of the pest in Canada brings the main part of the paper to a conclusion.

11. As a result of this investigation the Canadian entomologists now have at their command the three English parasites of the pea moth, together with those from an allied species—*Cydia molesta* (the oriental fruit moth)—already in Canada. Two parasites from this latter host have completed their development on *Cydia nigricana* in the laboratory, and it is hoped that the whole, or part, of this combined parasite complex will eventually effect a satisfactory measure of control of this troublesome and destructive pest.

8. Acknowledgments.

The writer wishes to express his thanks to Dr. W. R. Thompson, Superintendent of Farnham House Laboratory, for helpful advice on several occasions, to the managers of those canning factories who so kindly placed various facilities at his disposal, and to Mr. R. J. Spittle for his invaluable assistance with the illustrations.

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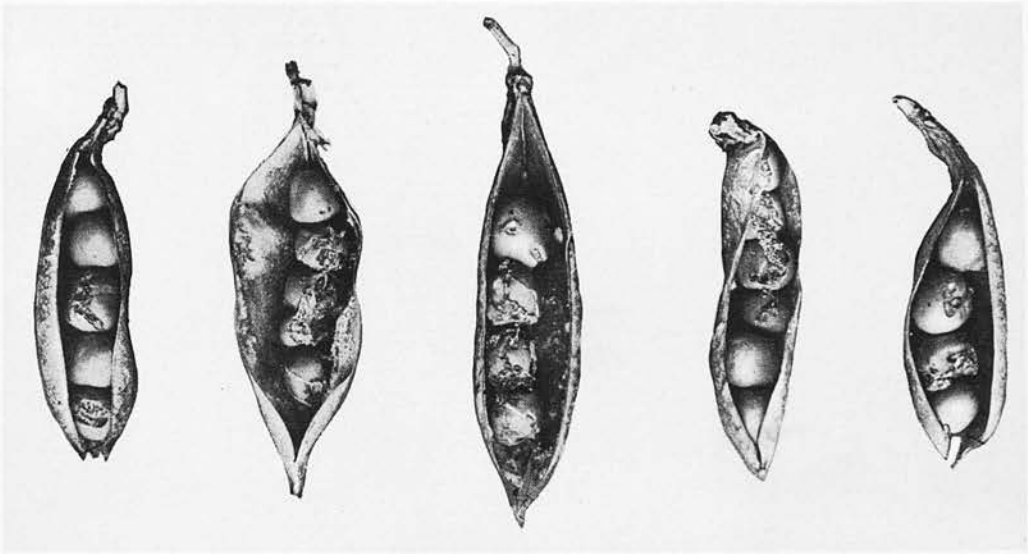

Fig. 1. Pea pods showing damage caused by the larvae of the moth, *Cydia nigricana*, Steph.

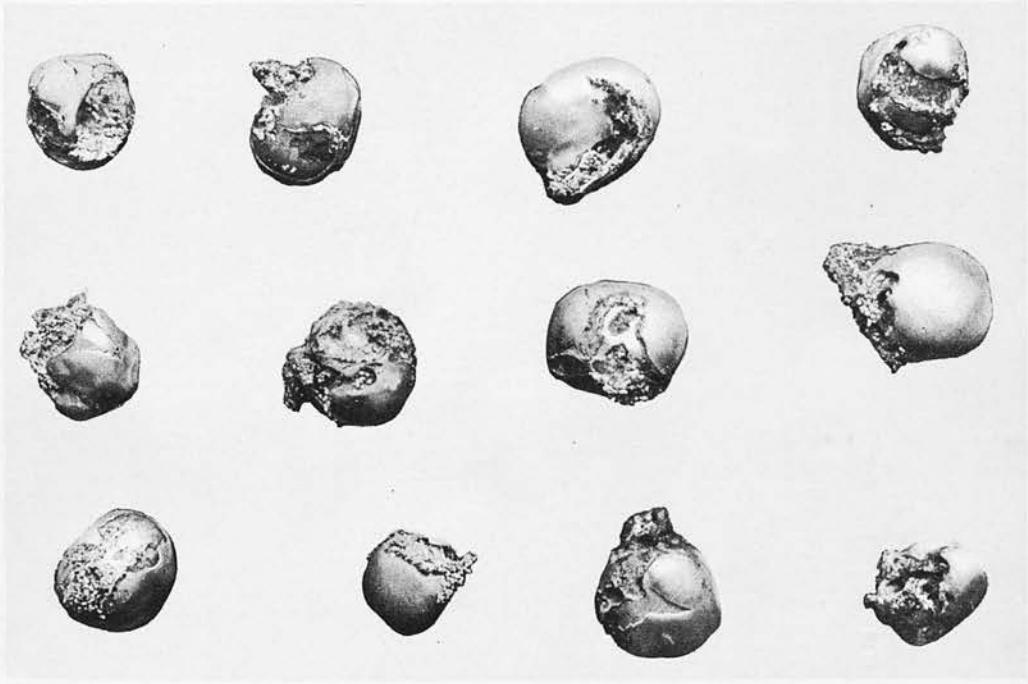

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Fig. 2. Infested peas. Note characteristic webbed excrement.

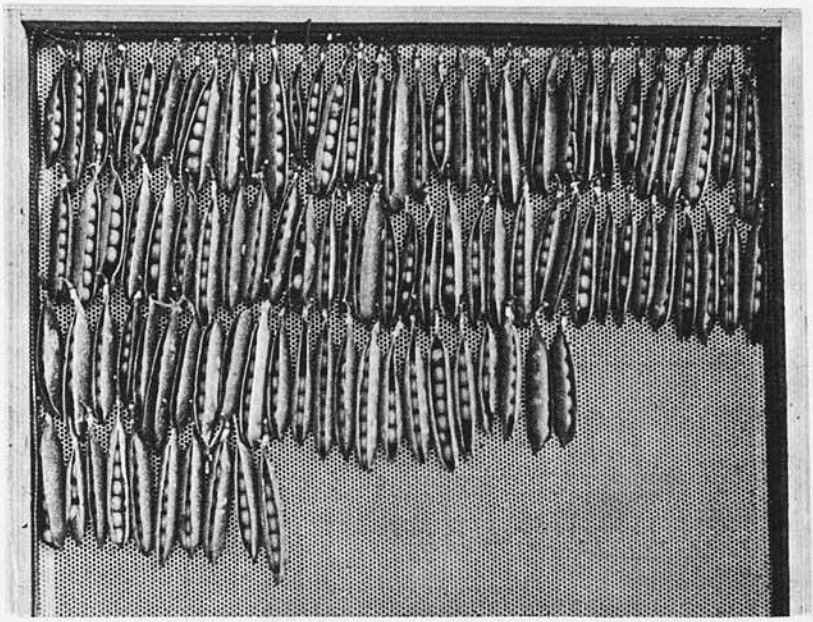

Fig. 1. Rearing tray with opened pea pods containing developing pea moth larvae.

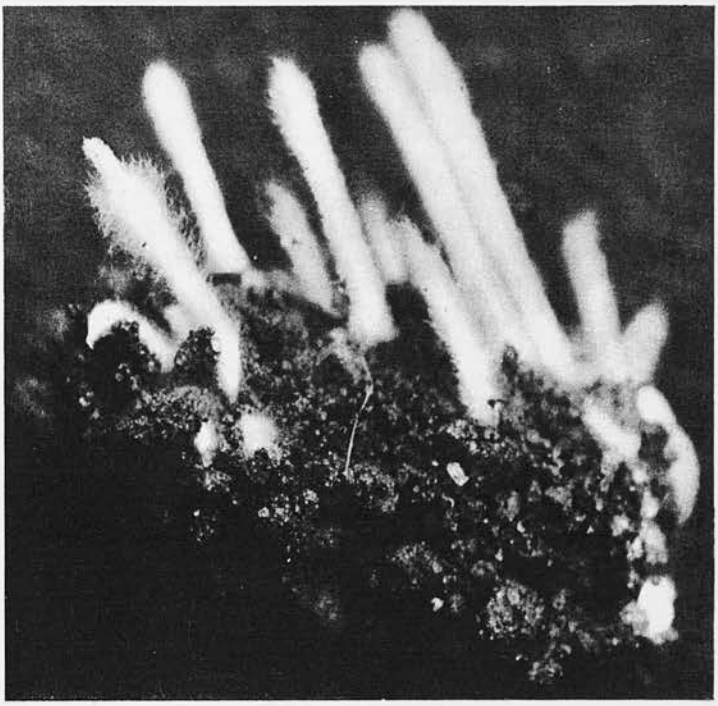

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Fig. 2. Cocoon of pea moth attacked by the fungus *Isaria farinosa*. Note peculiar club-shaped sporangia.

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THE BIOLOGY AND POST-EMBRYONIC DEVELOPMENT OF *OPIUS ILICIS* N.SP., A PARASITE OF THE HOLLY LEAF-MINER (*PHYTOMYZA ILICIS* CURT.)

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(With Plate ± and 8 Figures in the Text)

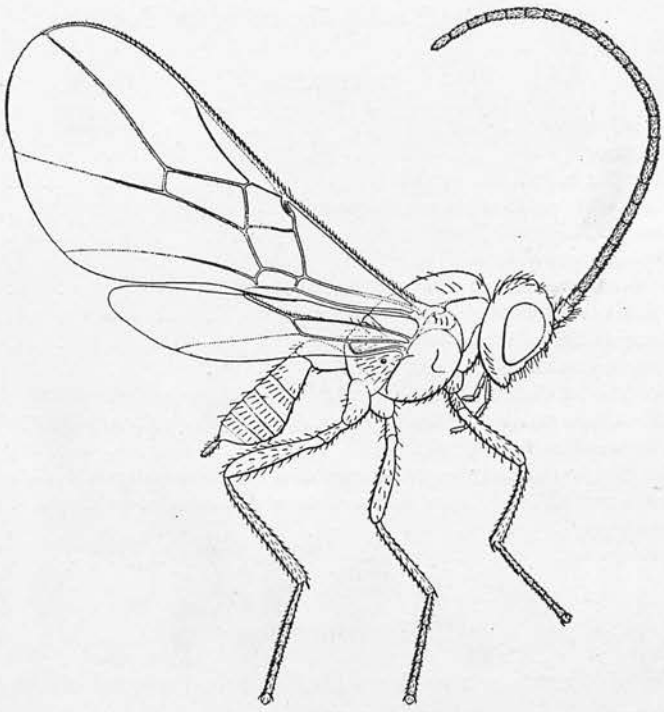
CONTENTS

I. INTRODUCTION

IN the course of the writer's work on the biological control of the holly leaf-miner (*Phytomyza ilicis* Curt.), an insect which has been causing considerable damage to holly in western Canada and other parts of the world, a new species of *Opius* was reared from several of the fly puparia. Although this Braconid is not a very common parasite of *Phytomyza ilicis* and on this account was only briefly mentioned in the author's previous paper (1939) dealing with the numerous Chalcid parasites of this host, yet it is of sufficient general interest, apart from the fact of its being new to science, to merit separate descriptive treatment. The present paper, therefore, gives a more or less complete account of its systematics, biology, morphology—more especially of the post-embryonic stages—anatomy, distribution, and host relationship. Its value as a parasite of the holly leaf-miner, the subject of interspecific competition, and some interesting phases of larval development which are of general entomological importance, are also discussed.

II. Systematic notes

Opius ilicis (Text-fig. 1) belongs to the family Braconidae, division Polymorphi, and tribe Opiinae. The Polymorphi, according to Marshall (1891), are characterized by the rigid suturiform articulation between the second and third abdominal segments, the unemarginate clypeus, and the cubital areolet, which is large, quadrangular, or wanting, but not minute, as in the Areolarii, while the Opiinae can be distinguished by the concave occiput, the three cubital areolets in the forewing, the axillary areolet which is without



Text-fig. 1. *Opius ilicis*, adult female (× 70).

a vestige of a transverse nervure, and the subsessile and ovate abdomen. *Opius* itself differs from the six remaining Opiine genera in the following particulars: the closed radial areolet, the radius, which springs from the base of the stigma; the second radial abscissa which is longer than the first intercubital nervure; and the narrow elongate stigma.

Mr G. Nixon, the Braconid expert of the Imperial Institute of Entomology, who examined the material I had reared, agreed at my suggestion to give this new parasite the specific name of *ilicis* Nixon, thus indicating its relationship with the host *Phytomyza ilicis*. The following short description of the imago, which was prepared by Mr Nixon and published recently in the

Entomologist's Monthly Magazine (1939), is reproduced here in order to complete the general account of the species:

"♂. ♀. Head brownish black above; the orbits, face, temples and cheeks pale brownish yellow; sometimes the face is suffused with darker colouring. Thorax brownish black; mesopleurae below sometimes suffused with reddish, as is also the mesosternum. Legs unicolourous, pale yellow. In examples caught wild the yellow colouring is more intense, almost ochreous, and the black patch on the top of the head tends to be reduced in size. On the whole there seems to be considerable variation in the colour of the head and the abdomen.

"♀. *Head:* Apex of clypeus widely separated from the mandibles. Mandibles with their lower margin simple; no trace whatever of an angulation near the base. Antennae with 23–29 segments (23–26 in 5 bred ♀♀; 26–29 in 9 wild ♀♀). *Thorax:* Notauli virtually wanting, showing anteriorly as short, deep, more or less smooth niches; the anterior margin of these niches is raised so that the mesonotum has prominent 'shoulders'. In bred ♀♀ the mesonotum is feebly longitudinally impressed; this feature is much less in evidence in wild examples. A few long hairs are present along the imaginary course of the notauli, especially posteriorly. No trace of a fovea against the posterior margin of the mesonotum. Posterior margin of the scutellum margined by a long, narrow, finely crenate groove. Mesopleurae with only a feeble, completely smooth impression. Propodeum predominantly smooth and shining. *Forewings:* radius leaving the stigma far proximal to middle; nervus parallelus arising from discoidalis very near middle of outer side of second discoidal cell. *Abdomen:* Petiole about one-and-a-half times as long as its apical width, finely rugose outside the area enclosed by the basal carinae and with a longitudinal element in the sculpture. Each of the tergites with a fairly even row of long cilia. Ovipositor projecting slightly beyond the apex of the abdomen.

"♂. Antennae with 25–28 segments (18♂♂).

"Length. ♂, ♀, about 1·8 mm.

"This species is superficially very like *Opius compar* Marshall, the type of which is in the British Museum. The most obvious differences between the two species are as follows: *O. compar* has the head thicker, less transverse, a small fovea against the posterior margin of the mesonotum, and the nervus parallelus arising from nearer the lower exterior angle of the second discoidal cell. I have not examined the mandibles of *O. compar* Marsh., since the only available specimen, the type female, is mounted flat on a card. Colour, that is the contrast between yellow and dark markings is a much more striking and characteristic feature of *O. ilicis* n.sp. than of *O. compar* Marsh., and is a very valuable guide to the identification of the species."

III. Distribution and host records

Specimens of *O. ilicis* were reared by the writer from holly fly material collected at Farnham Royal, Bucks; Windlesham, Surrey; Sunninghill, Berks; and the New Forest in Hampshire. This parasite was most abundant at Windlesham, Surrey, in an area where holly was associated with Scots pine. The parasitism in this area in 1939 averaged 4%, that is to say four *Opius* adults emerged from one hundred mines. By dissection in the early spring, however, 7% of the host larvae were found to be parasitized, but this figure, as a result of the pressure exerted by the intrinsically superior Chalcid, *Chrysocharis gemma*, was ultimately reduced to 4%. At Farnham Royal not more than 1% of the mines were attacked, and in several other areas, including Burnham Beeches in Buckinghamshire, *Opius ilicis* was not represented in the sample collections. From the very large consignments of holly fly material shipped to Canada from the latter region in 1939, however, a few specimens of this parasite were obtained (11 out of 100,000 mines), and this would seem to indicate that although *O. ilicis* is very rare in certain holly areas, it is, nevertheless, not completely absent from them.

The distribution of the genus *Opius* is world-wide, and numerous Opiine species have been reared from a large number of hosts in all five continents. In temperate regions the insects which suffer most from their attacks are species of *Pegomyia*, *Agromyza*, *Rhagoletis*, *Phytomyza* and *Cerodonta*, whilst in tropical and subtropical areas the most favoured hosts belong to one or other of the two genera *Dacus* and *Anastrepha*. It should be noted that all these insects are members of the order Diptera. Further host records are included in the succeeding section.

IV. Host relationship of the genus *Opius*

"The Opiinae", states the Rev. T. A. Marshall in his admirable *Monograph of British Braconidae* (1891), "is one of the most neglected of all Hymenopterous tribes." Why this should be so is not quite clear, for this group contains an interesting, and from the economic point of view, a very important collection of parasites. It is therefore to be hoped that the following data on the host relationship of the genus *Opius*, which has been collected for, among other reasons, the assistance of workers on Opiine species, will help to direct the attention of taxonomists towards them, and thus lead to a better arrangement of the whole group.

Specialists in the Braconidae are generally agreed that the genus *Opius*, as it stands at present, contains a large number of incorrectly determined species, some of which almost certainly belong to quite different genera, while several more have probably been given wrong generic names, so that a lot of taxonomic work still remains to be done before the various members of this large genus can be considered to have been satisfactorily classified. It is the

opinion of the present writer that a good general knowledge of the host relationship of the known species of a genus, that is, in so far as the parasites have been reared from their hosts and the relationship recorded in the literature, will be of great value to the systematist, especially when he is faced with the determination of doubtful and aberrant species. After all, the ideal scheme of classification should, if at all possible, take into account not only morphological, but also physiological and particularly ecological data, and it is with this conception in mind that the following list of host records for the genus *Opius* has been compiled. But apart altogether from classification the subject of host relationship is extremely interesting, especially from the economic standpoint, and any increase in our knowledge of the type of hosts attacked by a particular group of parasites is bound to be of sound practical value to the worker in biological control. This is especially true of the genus under review because of the very large number of economic pests which its members attack.

In the following list which has been compiled from various sources, including the Farnham House Catalogue, Leonardi, Essig, etc., there are 205 host records. The number of identified species involved is ninety-one, while twenty-one more are simply recorded as *Opius* sp. In the host list are included representatives of the five chief orders of the Insecta—Diptera, Lepidoptera, Coleoptera, Hemiptera, and Hymenoptera. By far the greatest number belong to the order Diptera, their relative abundance being as follows:

(1) Diptera with 182 records.
(2) Lepidoptera with twelve records.
(3) Coleoptera with nine records.
(4) Hemiptera with one record.
(5) Hymenoptera with one record.

The genera which suffer most heavily from the attacks of these parasites in the order of their frequency are as follows: (1) *Pegomyia* (36 records); (2) *Agromyza* (29 records); (3) *Dacus* (25 records); (4) *Ceratitis* (16 records); (5) *Rhagoletis* (10 records); (6) *Phytomyza* (9 records); (7) *Anastrepha* (8 records); (8) *Cerodonta* (4 records); while the most heavily attacked species are the Anthomyiid, *Pegomyia hyoscyami*, whose larvae mine the leaves of beet and mangold, and the Trypetid, *Dacus oleae*, the immature stages of which feed on the fruit of the olive tree. From the former, fourteen distinct species of *Opius* have been reared, in countries as widely separated as England, Germany, Sweden, Holland, Belgium, Russia, Italy, Canada, and the United States of America, while from the latter six species are recorded, mostly from the Mediterranean littoral, South Africa and India. It is particularly interesting to notice that the larvae which are attacked by the various species of *Opius* can usually (but not always) be found in one of two particular types of habitat. For the most part they are either leaf-miners or feeders inside fruits.

In the following list, all hosts not otherwise indicated, belong to the order Diptera:

Opius afreutretae Wlkn.
South Africa: *Acanthiphilus muiri* Bezzi, *Afreutretae bipunctata*, and *A. discoidalis* Bezzi.

Opius africanus Sz.
Italy, Eritrea, and South Africa: *Dacus oleae* Gmel.

Opius africanus var. *orientalis* Silv.
Eritrea and South Africa: *Dacus oleae* Gmel.

Opius agromyzae Vier.
Italy: *Agromyza nigripes* Mg. North America: *A. pusilla* Mg.

Opius ambivius Gour.
France and Italy: *Phytomyza ancholiae* R.-D. France: *P. xylostei* R.-D.

Opius anastrephae Vier.
Porto Rico: *Anastrepha* sp. Jamaica and Porto Rico: *A. fraterculus* Wied. U.S.A.: Trypetid species.

Opius anthomyiae Ashm.
U.S.A.: Anthomyiid species. North America: *Pegomyia bicolor* Wied. and *P. hyoscyami* Panz.

Opius aridis Gahan
North America: *Agromyza pusilla* Mg. U.S.A.: *A. scutellata* Fall., and *Cerodonta dorsalis* Lw.

Opius arisanus Sonan
Formosa: *Chaetodacus ferrugineus* var. *dorsalis* Hendel, and *Dacus dorsalis* Hend.

Opius bellus Gahan
Panama Canal Zone: *Anastrepha fraterculus* Wied.

Opius betae Bengtsson
Sweden: *Pegomyia hyoscyami* Panz.

Opius bremeri Bengtsson
Germany: *Pegomyia hyoscyami* Panz.

Opius bruneipes Gahan
North America: *Agromyza pusilla* Mg.

Opius brunneus Gour.
Italy: *Coleophora serenella* Z. (Lepidoptera).

Opius carbonarius Nees
Germany and Sweden: *Pegomyia hyoscyami* Panz.

Opius carinatus Thoms.
Germany: *Plodia interpunctella* Hb. (Lepidoptera).

Opius carpomyiae Silv.
India: *Carpomyia vesuviana* Costa and Trypetid species.

Opius caudatus Wesm.
France: *Callidium* sp. (Coleoptera) and *Pogonochaerus* sp. (Coleoptera). Italy: *Pogonochaerus hispidis* L. (Coleoptera), and *Pyrrhidium sanguineum* L. (Coleoptera).

Opius cereus Gahan
Trinidad: *Anastrepha serpentina* Wied. and *A. striata* Schin.

Opius cingulatus Wesm.
Europe: *Agromyza morio* Bris. Britain: *Acidia heraclei* L.

Opius compensans Silv.
India: *Dacus incisus* Wlk.

Opius concolor Sz.
Eritrea: *Carpomyia incompleta* Beck. Palestine, Tripoli, Algeria, Morocco, Italy, France, Greece, North Africa, and Tunisia: *Dacus oleae* Gmel.

Opius coriaceus Gahan
North America: *Cerodonta femoralis* Mg. U.S.A.: *C. dorsalis* Lw.
Opius cosyrae Wlkn.
Tanganyika: *Ceratitis cosyra* Wlk.
Opius cupidus Gahan
U.S.A.: *Pegomyia hyoscyami* Panz.
Opius dacicida Silv.
Italy, Eritrea and Transvaal: *Dacus oleae* Gmel.
Opius diastatae Ashm.
North America: *Agromyza parvicornis* Lw.
Opius dimidiatus Ashm.
U.S.A.: *Agromyza* sp., *A. pusilla* Mg., *A. scutellata* Fall. and *Cerodonta dorsalis* Lw.
Opius downesi Gahan
North America: *Rhagoletis pomonella* Walsh.
Opius ferrugineus Gahan
Canada: *Rhagoletis cingulata* Lw. and *R. fausta* O.S. U.S.A.: *R. pomonella* Walsh.
Opius fijiensis Fullaway
Fiji: *Dacus* sp., *D. passiflorae* Frogg., and Trypetid species.
Opius fletcheri Silv.
India: *Bactrocera cucurbitae* Coq. and *Carpomyia vesuviana* Costa. Hawaii, India, Loochoo Is., and Malaya: *Dacus cucurbitae* Coq. Malaya: *D. ferrugineus* F.
Opius foersteri Gahan
U.S.A.: *Eulia velutinana* Wlk. (Lepidoptera).
Opius formosanus Fullaway
Formosa: *Chaetodacus ferrugineus* F., *C. ferrugineus* var. *dorsalis* Hendel, and *Zeugodacus synnephes* Hendel.
Opius foveolatus Ashm.
North America: *Pegomyia hyoscyami* Panz.
Opius fulvicollis Thoms.
Belgium: *Pegomyia hyoscyami* var. *Betae* Curt. Sweden, Germany, U.S.A., North America, Holland and Belgium: *P. hyoscyami* Panz.
Opius geniculatus Thn.
Germany: *Stemnocera abrotani* Mg.
Opius giffardi Silv.
Tanganyika: *Ceratitis capitata* Wied.
Opius graccus Wesm.
Italy: *Nematus quercus* Htg. (Hymenoptera).
Opius humilis Silv.
Hawaii, Bermuda, Tunis, Spain, Kenya, Africa, and Hawaii to Australia: *Ceratitis capitata* Wied. Kenya: *C. cosyra* Wlk. Hawaii: *Dacus cucurbitae* Coq. U.S.A.: *Rhagoletis suavis completa* Cress.
Opius hyoscyamiellus Vier.
Canada: *Pegomyia hyoscyami* Panz.
Opius incisi Silv.
India: *Dacus incisus* Wlk.
Opius insularis Ashm.
Porto Rico: *Agromyza* sp.
Opius irregularis Wesm.
France: *Pegomyia acetosae*. Italy: *P. abbreviata* Pck.
Opius lantanae Bridw.
Hawaii: *Oscinis* sp.

Opius lectoides Gahan
U.S.A.: *Rhagoletis pomonella* Walsh.

Opius lectus Gahan
U.S.A.: *Rhagoletis pomonella* Walsh.

Opius leptostigma Wesm.
Italy: *Phora tuberum* Gour.

Opius longistigmus Gour.
France: *Phora tuberum* Gour.

Opius makii Sonan
Formosa: *Chaetodacus ferrugineus* var. *dorsalis* Hendel and *Dacus dorsalis* Hendel.

Opius mandibularis Gahan
North America: *Phytomyza chrysanthemi* Kowarz. U.S.A.: *Pegomyia pusilla* Mg.

Opius melleus Gahan
U.S.A.: *Rhagoletis mendax* Curran and *R. pomonella* Walsh.

Opius mellipes Prov.
Italy: *Cuephasia incertana* Tr. (Lepidoptera).

Opius nitidulator Nees
Czechoslovakia: *Calliphora vomitoria* L., *Lucilia caesar* L., *Musca domestica* L., *Pegomyia hyoscyami* Panz., *P. hyoscyami* var. *betae* Curt., and *Plusia gamma* L. (Lepidoptera). France: *Chortophila chenopodii* and *Tachina* sp. Britain: *Heliodines roesella* L. (Lepidoptera) and *Pegomyia hyoscyami* Panz. Belgium: *Pegomyia hyoscyami* Panz. and *P. hyoscyami* var. *betae* Curt. Sweden, North America, Germany, Russia and Italy: *Pegomyia hyoscyami* Panz.

Opius obscurator Ratz.
Italy: *Aphis rosae* L. (Hemiptera).

Opius ochrogaster Wesm.
France: *Lithocolletis geniculella* (Lepidoptera).

Opius oscinidis Ashm.
North America: *Phytomyza plantaginis* R.-D.

Opius otiosus Gahan
North America: *Agromyza parvicornis* Lw.

Opius pallidipes Wesm.
Italy: *Acidia caesto* Harr., *A. heraclei* L., *Agromyza macquarti*, *Pegomyia bicolor* Wied., *P. nigritarsis* Zett., and *Tortrix rosana* L. (Lepidoptera). France: *Agromyza macquarti*, *Anthomyia* sp., and *Tephritis* sp. Britain: *Tortrix rosana* L. (Lepidoptera).

Opius pegomyiae Gahan
North America: *Pegomyia hyoscyami* Panz. U.S.A.: *P. vicina*.

Opius perproximus Silv.
Tanganyika: *Ceratitis* sp., *C. cosyra* Wlk. Kenya: *C.* sp., *C. capitata* Wied., *C. cosyra* Walk., and *Dacus* sp. Sierra Leone: *C. giffardi* Bezzi and *C. punctata*. Zanzibar and West Africa: *Dacus ciliatus* Lw.

Opius perproximus modestor Silv.
Kenya: *Ceratitis nigra* Graham.

Opius persulcatus Silv.
Malaya: *Dacus ferrugineus* F. India: *D. incisus* Wlk.

Opius phaeostigma Wlkn.
South Africa and Mauritius: *Dacus ciliatus* Lw. and *D. d'emmerezi* Bezzi.

Opius phorelliae Wlkn.
Transvaal: *Phorellia peringueyi* Bezzi.

Opius polyzonius Wesm.
Europe: *Agromyza albitarsis* Mg. and *A. labiatarum* Hard.

Opius ponerophagus Silv.
India: *Dacus oleae* Gmel.
Opius procerus Wesm.
Europe: *Hylemyia antiqua* Mg. and *Phorbia brassicae* Bch. Sweden: *Pegomyia hyoscyami* Panz. Germany: *P. nigritarsis* Zett.
Opius pumilio Wesm.
France: *Anthomyia verbasci.* Italy: *Pegomyia bicolor* Wied.
Opius pygmaeator Nees
France and Italy: *Anthonomus sorbi* Germ. (Coleoptera).
Opius quebecensis Prov.
North America: *Pegomyia calyptrata* Zett. and *Scaptomyza adusta* Fall.
Opius reconditor Wesm.
France: *Agromyza xylostei* R.-D.
Opius reconditus Wesm.
Italy: *Acidia caesio* Harr. and *Phytomyza xylostei* R.-D.
Opius rhagoleticolus Sachtl.
Germanyand Switzerland: *Rhagoletis cerasi* L.
Opius rubriceps Ratz.[1]
Italy: *Magdalis ruficornis* L. and *M. violacea* L. (Coleoptera).
Opius ruficeps Wesm.
France: *Agromyza abiens, Pegomyia conformis.* Germany, Russia and Italy: *Pegomyia hyoscyami* Panz. Belgium: *P. hyoscyami* Panz. and *P. hyoscymai* var. *betae* Curt. Yugoslavia: *Pegomyia nigricornis* Strobl.
Opius rufipes Wesm.
France: *Acidia heraclei* L., *Agromyza mobilis, Lonchaea nigra* Mg., and *Pegomyia acetosa.* Italy: *Agromyza abiens* Zett., *Coleophora corrucipennella* Z. (Lepidoptera), *Domomyza mobilis* Mg., *Elachista griseella* Z. (Lepidoptera), *Lonchaea nigra* Mg., and *Pegomyia hyoscyami* Panz. Britain: *Coleophora nigrocella* Steph. (Lepidoptera).
Opius siculus Monastero
Sicily: *Dacus oleae* Gmel.
Opius spinaciae Thn.
Germany: *Pegomyia betae, P. hyoscyami* Panz. Belgium: *P. hyoscyami* Panz. and *P. hyoscyami* var. *betae* Curt. Sweden, Germany and Holland: *Pegomyia hyoscyami* Panz.
Opius straminator Gour.
Italy: *Orchestes fagi* L. (Coleoptera).
Opius stramineipes Thoms.
Europe: *Agromyza albitarsis* Mg.
Opius striativentris Gahan
U.S.A.: *Phytomyza ilicicola* Lw. and *P. ilicis* Curt.
Opius succineus Gahan
North America: *Agromyza* sp., *A. parvicornis* Lw., and *A. pusilla* Mg.
Opius suturalis Gahan
North America: *Agromyza pusilla* Mg., and *A. scutellata* Fall.
Opius sylvaticus Hal.
Sweden: *Pegomyia hyoscyami* Panz.
Opius testaceus Wesm.
France: *Euphranta connexa* F. and *Gonyglossum wiedmanni* Mg. Italy: *G. wiedmanni* Mg.
Opius tibialis Ashm.
U.S.A.: *Agromyza melanopyga* Lw.

[1] Marshall states that *O. rubriceps* Ratz. should be included in the genus *Cenocoelius.*

Opius trinidadensis Gahan

Trinidad: *Anastrepha serpentina* Wied. and *A. striata* Schin.

Opius utahensis Gahan

North America: *Agromyza parvicornis* Lw.

Opius wesmaeli Hal.

Sweden: *Pegomyia hyoscyami* Panz.

Opius zylostei Marsh.

France: *Phytomyza xylostei* R.-D.

Opius sp.

Hawaii: *Agromyza* sp. U.S.A.: *Agromyza scutellata* Fall., *Phytomyza delphiniae* Frost. Brazil: *Anastrepha fraterculus* Wied. Tanganyika: *Ceratitis* sp., and *Dacus humeralis* Bezzi. Uganda and Zanzibar: *Ceratitis* sp. Sierra Leone: *Ceratitis annonae* Wlk. and *C. coffeae* Bezzi. Kenya: *Ceratitis colae* Silv., *C. nigra* Graham and *C. rubivora* Coq. Korea: *Chlorops oryzae* Mats. Ceylon: *Dacus cucurbitae* Coq. French Cameroons: *Dacus humeralis* Bezzi. Fiji: *Dacus passiflorae* Frogg. and *D. xanthodes* Broun. America: *Eucosma ocellana* F. (Lepidoptera), and *Pegomyia hyoscyami* Panz. India: *Oscinis theae* Big. Germany: *Pegomyia hyoscyami* Panz. Java: *Promecotheca niciferae* Maulik (Coleoptera). Canada: *Rhagoletis pomonella* Walsh.

V. General biology of *Opius ilicis*

The imagines of *O. ilicis* emerge from the host puparia in the latter half of May and the beginning of June. In 1939, the first specimen to emerge from material collected in the Windlesham area—a male—was observed on 13 May and the last—a female—on the 30th of the same month. Because of the intimate connexion between the development of the *Opius* larvae and the pupation of the host, a point which will be explained more fully in a later paragraph, the emergence of the parasites follows very closely on that of the flies. In the area already mentioned, flies began to emerge on 11 May and continued to come out until the 25th of the month, a period which is only 2–5 days in advance of the *Opius* emergence dates. At Windlesham, females were more common on the whole than males. Out of twenty-three specimens reared from this area in 1939, fifteen were females and eight were males, which would give a sex ratio of 2 ♀♀ to 1 ♂, or 0·5, but the numbers obtained were so small as to make any generalization on this point untrustworthy. Indeed somewhat different figures were obtained in 1937 from a large collection of mined holly leaves, made in the New Forest, Hants. Soon after the arrival of this consignment in Canada flies and parasites began to issue from the mines, and by the end of the emergence period a total of ninety *Opius* adults were obtained. Of these forty-six were females, and forty-four males, so that in this area, and in this season, the sexes were present in about equal numbers.

Mating is a simple affair. No preliminary courtship takes place as in some of the Chalcidoidea and other groups, but the male, when aware of the presence of the female, moves his wings rapidly up and down as if preparing for flight, and then sets off in pursuit. On catching up with her, he mounts rapidly, and copulation, which lasts for only a few seconds, is quickly effected. Oviposition was not observed, but the following remarks give some indication

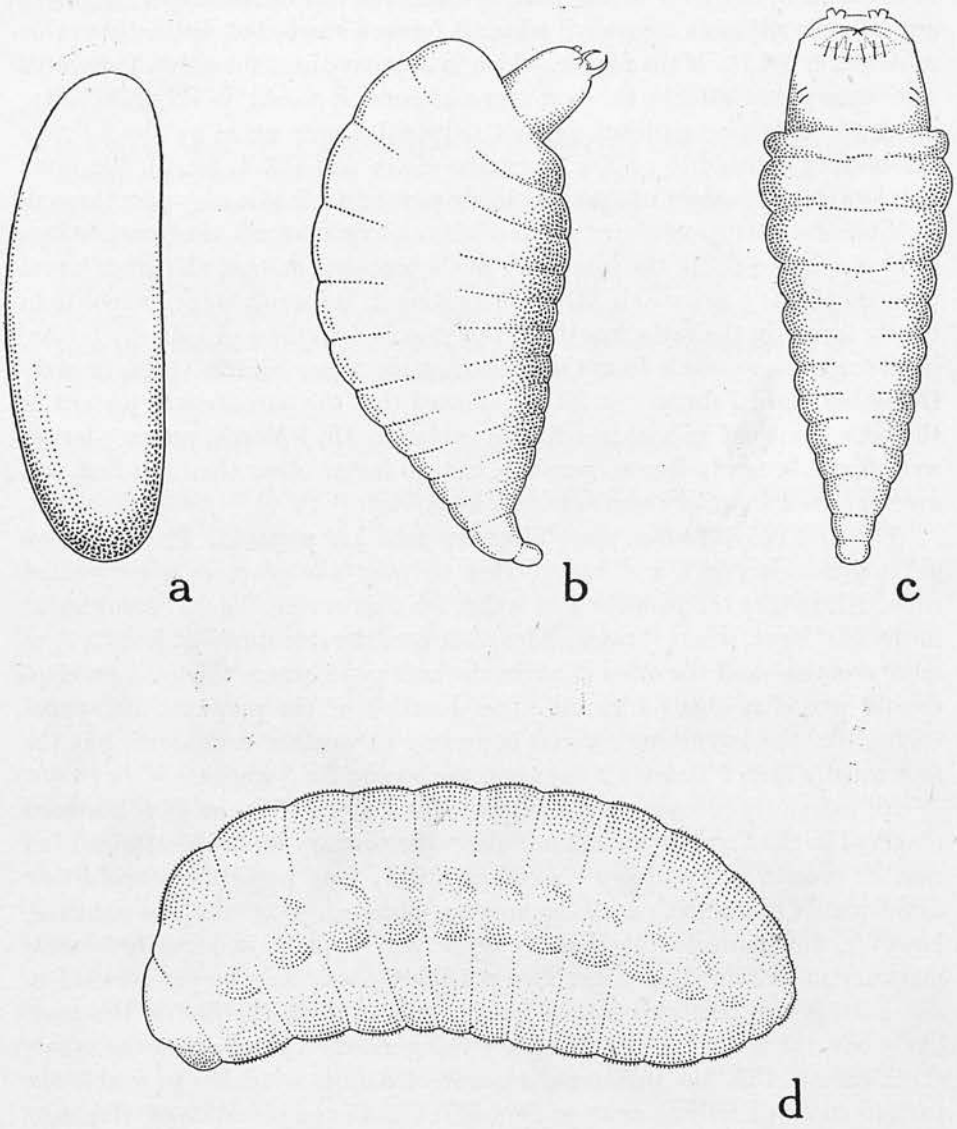
as to the time when it is most likely to take place. The two possible periods are midsummer (June) and midwinter (probably early December). In June the larva of the leaf-miner is extremely small and is hidden away in the vessels of the midrib, but later in the year, towards the end of November, it moves out into the adjacent mesophyll where it forms a small, but distinctly visible mine (Pl. I, fig. 1). If the female, which in captivity lives for only a few weeks after emergence, attacks the host larva in June, it would, in all probability, do so through the small but distinct oviposition scar made by the fly near the base of the midrib on the underside of the leaf (Pl. I, fig. 3). We must not, however, lose sight of the more likely possibility that it may pass through an alternate host, overwinter as an adult, and then attack the young mines in December, much in the same way as *Chrysocharis gemma*, the other larval parasite of this host, which, after hibernating in the adult stage, oviposits in the fly larvae in the early months of the year. Dissections of holly-fly larvae, in all three stages, made from the time when the mines became visible in early December, until February or March, showed that the parasite was present in the body cavity of its host as a first stage larva. On 7 March, primary larvae were found in newly formed puparia, but no instar other than the first was ever obtained from any stage of the host larva.

The first ecdysis takes place after the host has pupated. From then on development is rapid, and two further ecdyses take place in a very short time. Altogether the parasite passes through four stages, the first being spent in the host larva, where it remains for some considerable time—at least 2, 3, or more months—and the other three in the host pupa, where the total developmental period is about 1 month. The duration of the prepupal and pupal stages, like the larval ones, varies according to weather conditions, but the first usually lasts for about 2 days and the second for 3 weeks.

An extremely interesting phase in the life history of *Opius ilicis* has been observed in the first larval stadium. After the primary larva has attained full size, its growth is retarded for a comparatively long period, and no further development takes place until the host has pupated. Once this has occurred, however, the parasite proceeds to grow very rapidly and reaches larval maturity in quite a short time. Two possible reasons may be put forward to account for this method of development and of these the first is the most likely one, the second in all probability being merely a corollary of the other: (1) it ensures that the maximum amount of food is available to enable the parasite to attain full size as an adult; had the latter completed its development in the host larva, undersized and stunted individuals, if any at all, would in all probability have resulted; (2) it enables the second and third larval instars to feed with the minimum of effort on the easily ingested histolysed tissues of the host. As a result of this method of feeding the cephalic skeleton in these two instars is very poorly developed, indeed it is so reduced that only traces of it can be observed and that with some difficulty.

O. ilicis is an internal solitary parasite of the holly leaf-miner, and although

it is very likely that, on occasion, several primary larvae may be found in the same host, only one ever attains to maturity.



Text-fig. 2. *Opius ilicis*, (*a*) egg (×500); (*b*) primary larva, side view (somewhat contracted); (*c*) primary larva, ventral view (*b* and *c* ×280); (*d*) mature larva (×70).

VI. DEVELOPMENTAL STAGES

The egg

The egg (dissected from a week-old female) is whitish in colour, smooth and kidney-shaped. It is rounded at both ends, one of which is broader than the other and measures 0·2 mm. in length by 0·06 mm. in maximum breadth (Text-fig. 2*a*).

The primary larva

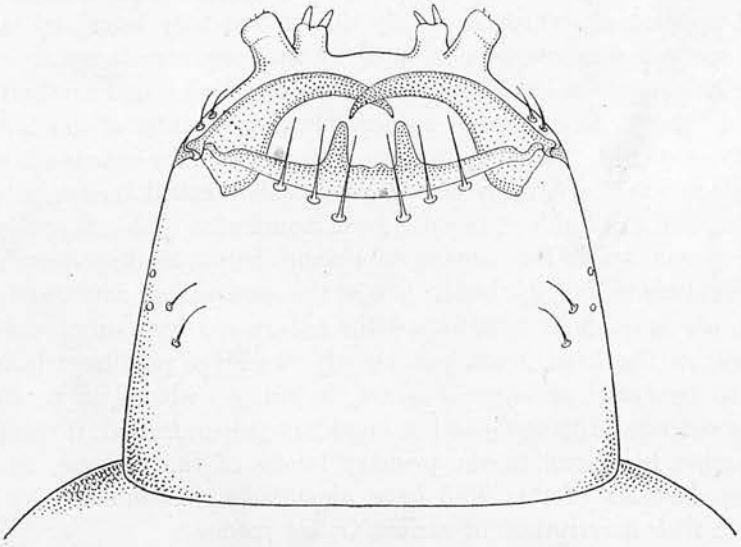
The primary larva of *Opius ilicis* is very typical in appearance and cannot possibly be confused with the corresponding stage of any other parasite of the holly leaf-miner. When viewed from the side (Text-fig. 2*b*) it has a peculiar humped appearance, which is mainly due to the very broad thorax. This unusual shape is somewhat accentuated by the narrow rectangular head and tapering abdomen, the last segment of which is curved round vertically in the form of a "tail". An extremely remarkable characteristic of this larva is its unusual orientation. Contrary to normal experience the concave side of the larva, which would ordinarily be regarded as the ventral surface, is actually the dorsal one. The truth of this can be demonstrated by locating the central nervous system which lies some little distance below the hypodermis on the *convex* (ventral) side of the body. Unless this exceptional curvature is borne in mind, one is liable to misinterpret the nature and position of some of the structures on the head, more particularly the large papillae which would appear to be dorsal antennae but are, in reality, ventral in position and probably correspond to the labial or maxillary palps. Indeed, if this peculiar conformation is general in the primary larvae of the Opiinae, as is very probable, mistakes of this kind have already been committed by certain authors in their descriptions of various Opiine species.

A similar type of orientation to that just described has been observed in the first stage larva of the related Braconid, *Diachasma crawfordi*, by Keilin & Picado (1913). These authors attributed this orientation to an uneven rate of growth, suggesting that the ventral side of the larva had grown more rapidly than the dorsal one. In *Opius ilicis*, and perhaps in other species of *Opius*, it is possible that the serosal cells (mentioned later) on the concave dorsal side may have some connexion with the abnormal curvature of the larva, but whatever the cause or significance of this strange phenomenon may be, it is certainly something very much out of the ordinary, and it cannot fail to be of great value for systematic purposes. Further demonstrations of its existence in other members of the Opiinae will therefore be awaited with much interest.

In dorsal view, the head of the primary larva of *O. ilicis* (Text-fig. 2*c*) is quadrate in shape, the thorax broad and the abdomen narrowly tapered. There are thirteen fairly well-defined body segments in addition to the head and the larva is semi-transparent. In the younger first stage larva a loose mass of

large serosal cells with large nuclei is attached to the concave dorsal side of the body, extending from the head to the posterior part of the abdomen in a similar manner to the serosa in the larvae of *O. humilis* and *O. fletcheri*, described by Pemberton & Willard (1918). These cells are absent in the older primary larvae. When fully grown the first stage larva measures: length 0·40 mm.; breadth at thorax 0·15 mm.; length of head 0·09 mm.; breadth of head at middle 0·09 mm.; length of mandibles 0·05 mm.

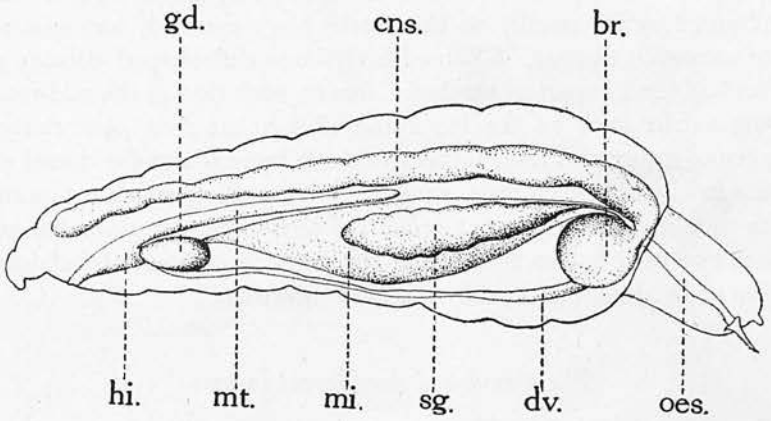
Traces of the two main tracheal trunks partially filled with gas were observed in the body segments, but no spiracles are present in this stage, so that the respiratory system is apneustic, and gaseous exchanges must obviously be effected cutaneously.



Text-fig. 3. *Opius ilicis*, head and cephalic skeleton of primary larva, antero-dorsal aspect (× 960).

A close examination of the head (Text-fig. 3) revealed several interesting features, notably the large falcate mandibles, each consisting of a triangular base and a long, curved, well-chitinized tip; the mandibular bar, which name I have applied to the stout rod extending across the head in front of the mandibles in the labroclypeal area; and the large, paired labial or maxillary papillae. Probably the most outstanding structure in the cephalic skeleton of this larva is the mandibular bar, which, as I have already stated, is a thick chitinized rod stretching across the face from one side of the head to the other. It is thicker in the middle and rather tapered towards the ends, and is chiefly remarkable for the very large vertical teeth—7·5μ in length—which project in a U-shaped manner from its centre. It is possible that these teeth are useful for steadying and locking in position the long, curved mandibles when the latter are employed in attacking rival larvae. Sometimes a third, small,

and insignificant tooth may be found between the two larger ones, but this is not invariably present. The superior mandibular strut, pleurostoma and hypostoma are very much reduced in this larva and are represented only by a small pleural sclerite on the wall of the head. This structure, which contains a relatively large socket, affords support to the inner and larger mandibular condyles. On the antero-ventral margin of the head there are two pairs of very large and prominent papillae, which are probably sensory in nature, and may be regarded as the labial or maxillary palps. The outer pair is slightly larger than the inner one—10·8μ in length compared with 6·5μ—and on the ends of both there are small spines, which are much larger and more conspicuous on the internal pair. The only other characters worthy of notice are the spines which, although rather long, are not particularly easy to see in



Text-fig. 4. *Opius ilicis*, side view of primary larva showing internal anatomy (semi-diagrammatic). Note particularly the position of the nerve cord on the *convex* ventral surface which demonstrates the unusual orientation of this larva (×480). *br.* brain; *cns.* central nervous system; *oes.* oesophagus; *dv.* dorsal vessel; *sg.* salivary gland; *mi.* mid-intestine; *mt.* Malpighian tubes; *hi.* hind-intestine; *gd.* gonad.

prepared slides, but can be discerned without much difficulty in physiological salt solution. These are situated in the following positions: two pairs near the mandibular articulation, three pairs in the clypeal region, and four pairs near the outer mid-dorsal margin of the head. A few scattered spines are also present on the body.

The internal anatomy of this larva (Text-fig. 4), because of the abnormal curvature of the head and body, is of more than passing interest. Most important are the positions of the central nervous system and the dorsal vessel. The former lies some little distance beneath the surface on the *convex* side of the larva, whilst the latter occupies a position between the intestine and the body wall on the *concave* side. The nervous system consists of two stout ganglionated longitudinal cords, which stretch from the first to the eleventh body segment. In the thoracic region the ganglia are rather larger than those in the abdomen, whilst the posterior ends of the cords are somewhat

club-shaped in appearance. From each pair of ganglia two stout transverse nerves are given off to supply the various organs of the body. The brain, which is united to the suboesophageal ganglia by a transverse commissure, consists of a pair of large subspherical ganglia situated in the first body segment and not, as is more usual, in the head. It occupies this position probably because of the relatively small size of the latter. The digestive system consists of the mouth, dilatable pharynx, and short oesophagus in the head, the large mid-intestine which occupies the greater part of the body cavity, and a short hind-intestine which terminates at the junction of segments ten and eleven. The hind-gut is often very dilated. An apparently open anus is present (it is possible, of course, that it is covered by a thin almost undiscernible membrane), but there is no open communication between the mid- and hind-intestines. The Malpighian tubes, which arise from the hind-gut are two in number. They extend forward usually to the fourth body segment, but occasionally they are somewhat shorter. A pair of fairly large club-shaped salivary glands are present in the forepart of the body, one on each side of the mid-intestine, extending as far back as the beginning of segment five. Anteriorly they narrow considerably and their respective ducts bend round the dorsal ganglia and unite in the head to form a common salivary duct, which communicates with the mouth. The only other organs of any importance are the gonads, which are two oval bodies situated in the posterior part of the abdomen in the region of the junction of mid- and hind-intestines.

The second and third larval instars

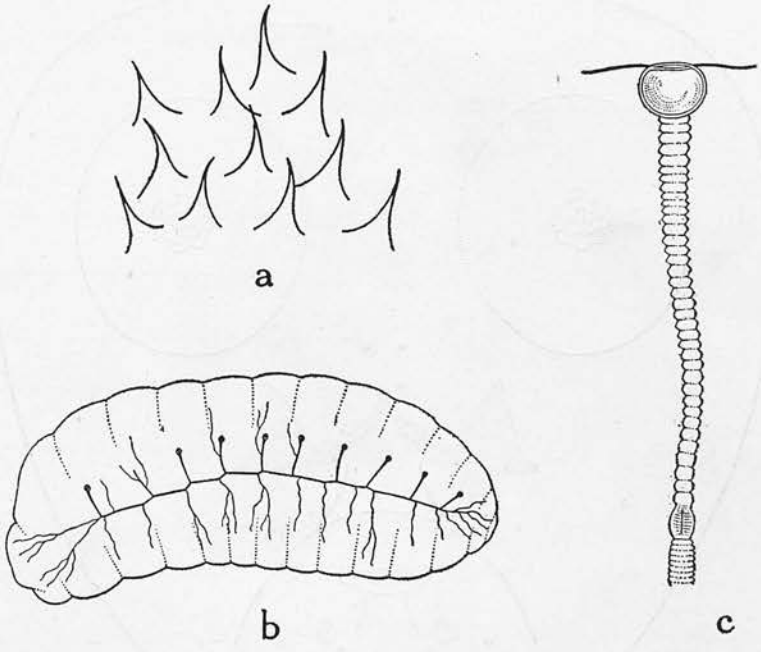
Both second and third stage larvae are characterized by extreme simplification of structure and the absence of chitinized areas. The second instar is somewhat fusiform in shape, with a hemispherical head and fairly well-defined body segmentation. It is for the most part transparent, save for the gut, which is full of brown material. The chief structures on the rather delicate head are two pairs of papillae, a larger outer and a smaller inner pair. The mandibles are present but, being unchitinized, they are extremely difficult to see. They are small with short tips and comparatively large bases. The only other features of any significance are the very large salivary glands which extend into the fourth body segment. Their respective ducts join to form an unusually short and broad common salivary duct just below the mouth. The "degenerate" cephalic skeleton in this and the succeeding instar and its relation to feeding, etc., has already been mentioned, and will be discussed again in a later section. No tracheal system was observed in this stage. The measurements of the second instar larva are as follows: length 0·8 mm.; maximum breadth 0·35 mm.

The third stage larva is very similar in appearance and structure to the second, and there is nothing remarkable to describe. Towards the end of this stage the tracheal system, spines, etc., of the fourth instar may be seen below

the skin. The mature third stage larva measures 1·2 mm. in length by 0·44 mm. in maximum breadth.

The mature larva

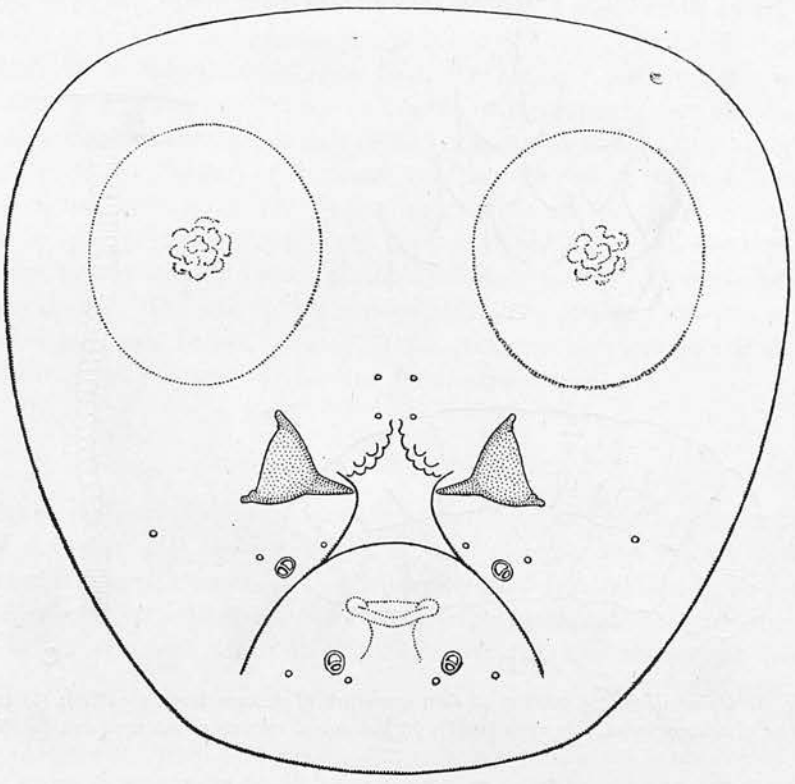
The mature larva (Text-fig. 2*d*), with some slight modifications, resembles in a general way the usual grub-like form common in the *Hymenoptera Parasitica*. It is rounded at both ends, and somewhat concave ventrally, while the thorax and abdomen are equally broad, a characteristicwhichreminds one of the larva of another Braconid, *Ascogaster quadridentatus*, described by the present writer in 1938. The head is conspicuous and the segmentation of the body is well marked. Altogether the body is divided into thirteen segments



Text-fig. 5. *Opius ilicis*, (*a*) portion of skin armature of mature larva (×1650); (*b*) trachea system of mature larva, side view (×67); (*c*) abdominal spiracle of mature larva (×1650).

(excluding the head), the last of which is rather small. In colour the larva is yellowish white, the yellow tinge being imparted by the gorged gut contents. The skin is characterized by a strong, dense armature of triangular spines, which are present all over the body, with the exception of the intersegmental areas. They are absent from the head. These spines (Text-fig. 5*a*), which measures 10μ in height by 7·2μ in diameter at the base, give the larva a decided shagreened appearance and this feature makes the identification of the fourth instar larva a relatively easy matter. A well-developed tracheal system (Text-fig. 5*b*), which is supplied by nine pairs of open spiracles situated on the anterior margins of segments 2 and 4–11, is present in this stage. These spiracles (Text-fig. 5*c*) consist of a rather small, subcircular atrium, 10·5μ

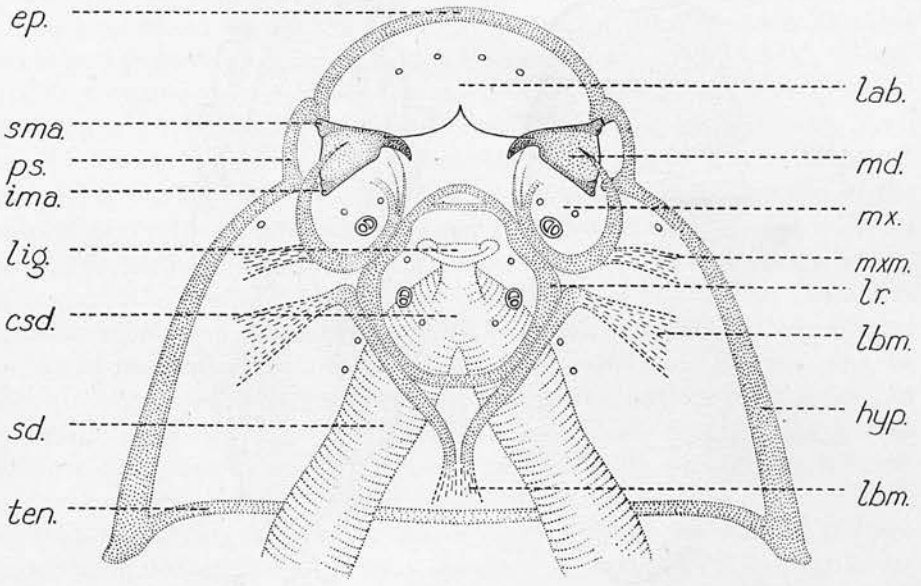
in breadth, 8·6 μ in depth, with an external aperture 5 μ in diameter, followed by a very long spiracular trachea composed of some 40–50 rings. At the inner end of this trachea there is a small swollen tube, which appears to be a closing device of some sort, similar in construction to that described in the Chalcid, *Sphegigaster flavicornis* (Cameron, 1938), another parasite of *Phytomyza ilicis*. The spiracular tracheae join on to the two main longitudinal trunks which extend through almost the entire length of the body, and are united by transverse commissures in segments 2 and 11. Spiracles are absent from the second thoracic segment, although the spiracular trachea itself is well developed.



Text-fig. 6. *Opius ilicis*, head of mature larva, antero-ventral view (× 600).

The head (Text-fig. 6), which is somewhat hemispherical in shape, is characterized by the usual lobes—two upper or epicranial, and one lower, median, or labial. On each epicranial lobe there is a large subcircular antennal area, which is slightly raised in the centre. Around the mouth, the mandibles, labrum, maxillae with slightly chitinized borders, and labium, together with a number of papillae, are the most prominent features. Closer examination reveals a well-developed, though weakly-chitinized, cephalic skeleton (Text-fig. 7). This consists of epistoma, pleurostoma, hypostoma, and tentorium, all unchitinized, a pair of small mandibles with curved chitinized tips, a complete

labial ring, inside which is a chitinized ligula and two 8-shaped papillae. A pair of similarly shaped papillae are present on the maxillae. The salivary ducts are extremely large, and the common duct formed by their union is very short and broad. In addition to the large "sensory" processes on the labium and maxillae, a number of smaller papillae are present in the following regions: on the labium, two pairs; on the maxillae, two pairs; within the labial ring, two pairs; below the latter, two pairs; and outside the maxillae, one pair; while the lower part of the labium is characterized by a roughened rasp-like structure. In this larva the muscles of the cephalic skeleton are rather well defined, especially those of the mandibles and maxillae, and particularly those of the labium.



Text-fig. 7. *Opius ilicis*, cephalic skeleton of mature larva (×600). *ep.* epistoma; *lab.* labrum; *ps.* pleurostoma; *md.* mandible; *mx.* maxilla; *mxm.* maxillary muscle; *sma.* superior mandibular articulation; *ima.* inferior mandibular articulation; *lr.* labial ring; *lbm.* labial muscles; *hyp.* hypostoma; *lig.* ligula; *csd.* common salivary duct; *sd.* salivary duct; *ten.* tentorium.

The measurements of the mature larva are as follows: length 1·4–2·3 mm., average 1·8 mm.; breadth of thorax and abdomen 0·5–0·8 mm., average 0·7 mm.; breadth of head 0·03 mm.

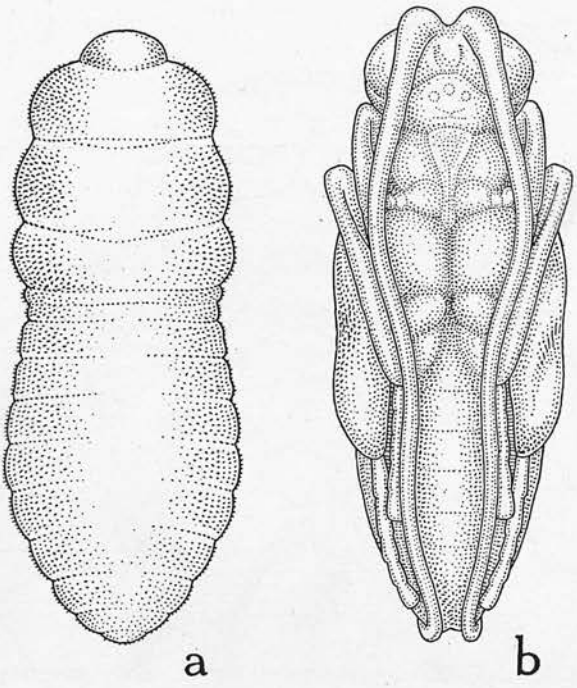
The prepupa

The prepupa (Text-fig. 8*a*), like the mature larva, is characterized by a dense skin armature of triangular spines. It differs from the latter in the constriction of the body into three definite regions: (1) the old larval head with its inconspicuous cephalic skeleton perched on the top of the first body segment—from these two segments, the pupal, and eventually the adult head,

will develop; (2) the thoracic region, consisting of two rather broad segments; and (3) the abdominal region, composed of the ten remaining segments. This instar is whitish grey in colour and its overall measurements are somewhat less than those of the mature larva.

The pupa

When newly formed the pupa (Text-fig. 8*b*) is white in colour, except for the eyes which have a light brown hue. It remains white for quite a long time after pupation has taken place, but towards the end of the pupal period, the



Text-fig. 8. *Opius ilicis*, (*a*) prepupa; (*b*) pupa. Note long antennae (*a* and *b* × 67).

head and thorax become black, the abdomen darkens, the wings and antennae change to dark grey, and the legs become straw-coloured. The pupa of *Opius ilicis* is very easily recognized by the long antennae, which extend down over the ventral surface of the body, and curve back over the posterior end on to the dorsum of the abdomen. With this useful character there can be no difficulty in distinguishing it from the pupae of all the other parasites of the holly leaf-miner.

VII. The comparative morphology of *Opiine* larvae

As previously indicated, the Opiinae, despite their great economic importance, have received comparatively little attention from systematists. A similar paucity of records exists so far as the biology and larval morphology

of the genus *Opius* is concerned. Probably the best accounts of the latter, to appear thus far, are those of Pemberton & Willard (1918), on *O. humilis* Silvestri, one of the Mediterranean fruit fly parasites, and of Willard (1920), who gave a useful description of the life history of *O. fletcheri* Silvestri, a parasite of the melon fly in Hawaii. The biology of *O. melleus* Gahan, which is parasitic on the blueberry maggot in the U.S.A., has also been very briefly recorded by Lathrop & Newton (1933), but in this case no figures or descriptions of the various larval stages are given. From one or two statements in this paper, however, it appears that the morphology of the latter species corresponds with that of *O. ilicis* in the two following particulars: the long, sharp, curved mandibles of the primary larva, and the absence of conspicuous appendages in the second and third instars. Further comparisons with *O. melleus* cannot be made because of the lack of data provided by these authors. The descriptions of Willard & Pemberton, and Willard, of *O. humilis* and *O. fletcheri* respectively, are very much fuller, but still incomplete. So far as the primary larvae are concerned these two species, like *ilicis*, are noteworthy for their possession of a mandibular bar complete with U-shaped projection. Indeed this feature, which is also present in two species of the related genus *Diachasma*, *D. tryoni* and *D. fullawayi*, would seem to be an extremely useful and general identification mark for primary Opiine larvae. The quadrate head and large falcate mandibles are two further characters which are common to the three species of *Opius* under consideration. Additional points of resemblance between *ilicis* and both *humilis* and *fletcheri* are: the mass of egg serosal cells which are attached to the early primary larva, the apneustic tracheal system and broad thorax of this stage; the apparent absence of tracheae in the second and third instars; the peripneustic tracheal system in the final instar; the well-developed cephalic skeleton of the primary and mature larvae, and the vestigial character of this structure in the two intervening instars; the large body spines on the skin of the mature larva; and, in the pupa, the very long antennae which extend over the full length of the body and curve back dorsally over the abdomen. The main differences between *ilicis* and the other two species are as follows: in the primary larva, (1) the absence of sac-like appendages on the antero-dorsal edge of the first body segment, which are present in both *humilis* and *fletcheri*; (2) the labial or maxillary papillae, of which there are two distinct pairs in *ilicis*, but in *humilis* and *fletcheri*, so far as can be made out from the diagrams, only one pair, whilst in the mature larva of *ilicis* the spines are more generally distributed over the body than in either of the other two species. No detailed descriptions of the cephalic skeleton are given by either of the authors mentioned, but a comparison of Text-fig. 7 in the present paper, and Willard's diagram (1920, p. 429), suggests that there is a labial strut in the mature larva of *O. fletcheri* which is not present in *O. ilicis*. This point, however, owing to the lack of detailed description and labelling of the diagram of *fletcheri*, cannot be stressed.

Further work on the larval morphology of other Opiine species could be undertaken with advantage, but that already done, including the descriptions in the present paper, would seem to indicate that the larvae of this tribe form a fairly homogeneous group. So far as can be ascertained at the moment, recognition of an Opiine larva depends on the following characteristics: in the primary stage (1) the quadrate head; (2) certain features in the cephalic skeleton, particularly the mandibular bar with its U-shaped protuberance; (3) the unusual orientation of the head and body (observed in *O. ilicis* and *Diachasma crawfordi*, but in all probability true also of the other species mentioned, although overlooked by Pemberton & Willard); in the second and third instars (1) the extremely simplified and unchitinized cephalic skeleton; (2) the apparent absence of tracheae; and (3) the lethargic disposition of the larvae: and, in the final instar, the dense armature of spines on the skin of the body. It is also possible that common characters exist in the cephalic skeleton of the mature larva, but further work and more detailed diagrams are necessary before useful comparisons can be made.

VIII. Value as a parasite of *Phytomyza ilicis*

Although by no means a common parasite of the holly leaf-miner, *Opius ilicis* was found to be present in small but appreciable numbers in most of the areas where collections of mined holly leaves were undertaken. This was particularly true of the Windlesham area where in 1939 its average parasitism was 4%. In certain other districts, however, notably Burnham Beeches, Bucks, where a vast quantity of material was collected, it was very much scarcer. As will be shown in the next part of this paper, *O. ilicis* is intrinsically inferior to *Chrysocharis gemma*, the other larval parasite of the holly leaf-miner, that is to say when the two as larvae come into conflict in the same host, the former succumbs, and the latter usually continues its development. Since this is so, those puparia from which *Opius ilicis* adults emerge represent hosts left unparasitized by *C. gemma*, so that in spite of the intrinsic superiority of the Chalcid, the total mortality in leaf-miner larvae resulting from the combined parasitism of the two species is greater than it would be if the *Chrysocharis* were acting alone. In the hosts where the two parasites conflict, the stronger and mor eabundant species survives and thus the efficiency of *Chrysocharis gemma*, which is the commonest parasite of *Phytomyza ilicis*, and the one which contributes most to the very high mortality which occurs in this host, is in no way impaired by the presence of its Braconid rival. There can therefore be no question as to the advisability of liberating this species in Canada, for any criticism of its usefulness, on the grounds that it competes adversely with a more efficient parasite, can be countered by the fact, that in all cases where the larvae of the two species were found in the same host, those of *Opius ilicis* were either dead or dying. From these remarks it will be gathered that this parasite, which is responsible for the elimination of a certain

number of hosts escaping the attention of other species, fills a particular niche of its own, and must therefore, even although the percentage of hosts which it accounts for is small, be of some definite value in the scheme of control. It is also possible that it may be even more efficient under the new conditions which exist in the holly areas of western Canada, where the holly leaf-miner is such a troublesome and annoying pest.

IX. COMPETITION WITH *CHRYSOCHARIS GEMMA*

The intrinsic superiority of the Chalcid *Chrysocharis gemma* over *Opius ilicis* has already been discussed, but the problem of the disposal of excess larvae in one and the same host, which is more difficult of solution, has yet to be examined. In the next part of this paper it is suggested that the large mandibles, mandibular bar teeth, etc., are valuable offensive weapons which enable the dominant larva of *O. ilicis* to emerge successfully from intraspecific combats. When the conflict is of an interspecific nature, however, and the primary larva of this species is involved in a fight with the corresponding stage of *Chrysocharis gemma*, the latter usually proves victorious. It is true that, owing to the comparative scarcity of host parasitized by *Opius ilicis*, the number of dissections carried out to prove this statement was somewhat limited, but nevertheless all actually undertaken pointed to the decided superiority of the Chalcid. When one considers the apparently superior armament and larger size of the latter (length of mandibles in *Opius* 0·05 mm., do. *Chrysocharis* 0·02 mm.; length of *Opius* larva 0·40 mm., do. *Chrysocharis* 0·30 mm.; maximum breadth of *Opius* larva 0·15 mm., do. *Chrysocharis* 0·08 mm.) this result is rather surprising. The method of elimination employed by the *Chrysocharis* parasite, judging by the injured and melanised Opiine larvae observed, is direct frontal attack. In one instance a host was found to contain an active primary larva of *Chrysocharis gemma* and a dead first stage *Opius* larva. The latter had its skin punctured both in the thoracic and abdominal regions. Significantly enough, these punctures were paired, suggesting that they had been caused by the opposing mandibles of the victorious Chalcid, whilst the areas surrounding the punctures were melanised, the dark colour probably being brought about by the oxidation of albuminoid substances in the blood and the precipitation of uranidine (*vide* Imms, p. 135).

Two possible reasons may be put forward to account for the marked inferiority of the Braconid: (1) despite its larger size, it is obviously very much less active than its wiry opponent, and this lethargic disposition may be attributed to two causes, (i) it is in a kind of diapause pending the transformation of the host into the pupal stage; (ii) it is older, and apparently less energetic than the more recently emerged and "metamorphically" vigorous *Chrysocharis*, and (2) it is possible that it may be partially paralysed as a result of the poison injected into the host by the Chalcid female prior to oviposition, and is thus less able to withstand the onslaught of its competitor.

This latter possibility will be more fully discussed in a moment. Although it would appear that the normal method of disposal employed by *C. gemma* is direct mandibular attack, this is not the only way in which the supernumerary larvae are eliminated. On one occasion a host was found to contain an active *Chrysocharis* larva and a dead first instar *Opius*. The latter bore no trace of melanised punctures or injury of any sort, and it seems quite possible that this larva owed its death to the poison injected by the *Chrysocharis* female. At any rate a comparison of the effects produced after parasitisation by each species suggests that this result may sometimes occur. When a host is attacked by *C. gemma* it very quickly changes from an active, turgid, bright, shiny, lemon-coloured larva to one which is paralysed, flaccid, and of a pale dirty yellow hue. A *Phytomyza* larva parasitised by *Opius ilicis*, on the other hand, or at least one containing a primary larva of this species, remains active, and no evident signs of parasitisation are apparent. If the poison injected by the *Chrysocharis* female is powerful enough to induce such a revolutionary change in the character of the host, it would appear equally possible for some sort of adverse effect to be produced on any *Opius* larva which may be present in the body cavity of a host subjected to this treatment. In certain instances it may be that death results, and in others the parasite may be paralysed and weakened to such an extent, that despite its apparently superior equipment, it becomes quite unable to compete successfully with its Chalcid rival.

It has been suggested by Spencer (1926), in the case of certain Aphid parasites, that all but one of the competing larvae are killed by a biochemical process of inhibition rather than by direct mechanical injury. This explanation is supported by Thompson & Parker (1930), who state that: "It is more probable as Spencer has suggested in the similar case of *Aphidius*, that at a certain moment, soon after hatching, the larvae begin to pour into the blood a cytolytic enzyme which affects the tissues of the host, and those of the younger larvae of *Eulimneria* itself." Whether this is the final solution to the problem or not, is not yet certain, but at any rate we can say, with some measure of assurance, that although mechanical injury would appear to be one method by which supernumerary larvae are eliminated, it is by no means the only one.

X. Some general considerations

A number of interesting points which have a general bearing on the study of parasite larvae will be discussed in this section in the following order:

(i) The function of the cephalic skeleton in successive instars.

(ii) A note on the taxonomic value of the cephalic skeleton in the parasitic Hymenoptera.

(iii) Respiration and the development of the tracheal system in *Opius ilicis*.

(iv) Arrested development in the Opiinae and some related forms.

(i) *The function of the cephalic skeleton in successive instars*

The composition of the cephalic skeleton in the four larval instars of *O. ilicis* has been described in some detail in Part VI. All that remains to be done here is to relate this composition and degree of development to function. In the first and fourth instars the system of facial rods is well developed, but in the second and third it has become so reduced as to be almost non-existent. The following reasons are now put forward to account to some extent for this marked divergence in development. In the first stage larva, the cephalic skeleton, with its massive mandibles and paired teeth (Text-fig. 3), would appear to be developed almost exclusively for offensive purposes. It is also possible that the mandibles may be of some use in tearing up portions of the fat body, but their main function seems to be the destruction of rival larvae. Since *O. ilicis* is a comparatively rare parasite of the holly leaf-miner, no examples of hosts containing more than one larva of this species were obtained, but in the common allied species, *O. fletcheri*, Willard (1920) noted that in hosts with more than one primary larva of this parasite, a struggle for survival took place. "Many cases have been observed", he states, "where there were only one living and from two to eight dead parasite larvae in the same host individual. This struggle takes place immediately after hatching and usually within four hours, all but one of the larvae of *Opius fletcheri* have been killed." In another species, *O. melleus*, described by Lathrop & Newton (1933), a similar destruction of excess larvae has been observed. It is therefore highly probable that the strong well-developed cephalic skeleton in the first stage larva of *Opius* is primarily designed for aggressive action.

In the second and third instars the cephalic skeleton has been so reduced that it is almost invisible. This extreme reduction would seem to be correlated with the feeding habits of these two stages. In the histolysed tissues of the host, food is available in a highly assimilable form, and in addition there are no rivals to fight at this period of the life history, because *Chrysocharis gemma* does not attack the puparium, and the pupal parasites *Sphegigaster flavicornis* and *Chrysocharis syma*, etc., have not yet appeared on the scene. There is therefore no apparent necessity for the facial rods to be highly developed in either the second or the third instars, and their presence at all, even in a reduced form, can be explained only on the grounds that the mandibles are of some use in directing or wafting particles of food into the mouth (any breaking up of particles which may take place is almost certainly accomplished by the chemical action of the saliva, and in this connexion the presence of extremely large salivary glands and broad ducts in these larvae is noteworthy), and that they provide a foundation on which the well-developed skeleton of the fourth instar may be built up.

In the mature larva the cephalic skeleton (Text-fig. 7), although not particularly robust, is nevertheless well developed. Its function in this stage appears to be the cleaning up of the more solid tissues which remain after all

the liquid nutriment has been absorbed. As no cocoon is formed, its development in this species can have no relation to spinning activities, etc. The marked development of the labial area in this instar is interesting from a systematic point of view, and will be discussed at some length in the following subdivision.

(ii) *A note on the taxonomic value of the cephalic skeleton in the parasitic Hymenoptera*

It has been pointed out in previous papers by the present writer (1938, 1939), that the cephalic skeleton, among other anatomical features, affords some very useful characters for the separation of species and of larger systematic groups. A comparison of this structure in representative parasites of the holly leaf-miner, *Opius ilicis*, for the Braconidae and *Chrysocharis gemma* and *Sphegigaster flavicornis* for the two Chalcid families, Eulophidae and Pteromalidae respectively, should therefore prove to be of general taxonomic interest. The most striking differences between these two classes occur in the mature larvae, but the earlier stages also provide points of distinction. In the primary instar the Braconid differs from the Chalcids: (1) in its peculiar orientation (*vide* p.); (2) in the possession of larger and more falcate mandibles (0·05 mm. in length, cf. 0·02 mm. in *Chrysocharis gemma*); (3) in the possession of a mandibular bar with two prominent teeth, which is not represented in the corresponding area of either *Chrysocharis* or *Sphegigaster*, unless this rod is considered to be equivalent to the epistoma; and (4) in the possession of a small pleural sclerite on the wall of the head (Text-fig. 3), and the absence of a hypostoma, which structure is present in the two Chalcid species.

In the intermediate instars the cephalic skeleton is fairly well developed in the Chalcids, but vestigial in the Braconid.

The main points of difference between the two groups in the mature larvae are to be found in the labial and maxillary areas. In the labial area of *Opius*, as in most Braconid and Icheumonid larvae, there is a circular sclerite which has been termed the labial ring (Text-fig. 7), a structure which is absent from the cephalic skeleton of the Chalcid representatives. Within the labial ring there are two 8-shaped processes which may possibly be sensory in nature. Some writers have considered them to be the analogues of the labial palpi of the adult, but this interpretation is somewhat questionable. A similar pair is present on the maxillae. These papillae, as well as the labial ring, are entirely wanting in the Chalcids. Probably the best distinguishing mark of Braconid and Ichneumonid larvae, as pointed out by Thompson (1930), is the presence (with certain exceptions) of these two structures, the labial ring and the labial and maxillary sensillae, while the absence of them affords a useful clue to the identification of the immature stages of the Chalcidoidea. Other distinctive marks in the cephalic skeleton, of a more subsidiary character, are the presence in the Ichneumonidae and Braconidae of labial and maxillary

struts, and a ligula, and their absence in the Chalcidoidea. Sometimes the mandibles of Braconid larvae are toothed, a character which is often a useful guide to this group, but in *Opius*, and probably in most of the smaller members of the family, they are simple and unpectinated.

(iii) *Respiration and the development of the tracheal system in* O. ilicis

In *O. ilicis* the tracheal system, instead of following the more usual type of development, is rudimentary in the primary larva (traces of the two main tracheal trunks partially filled with gas have been observed in the body segments), highly developed in the final instar (Text-fig. 5*b*), and apparently wanting in the two intervening stages. It is possible, of course, that fluid-filled tracheae are present in these larvae, but this is a point which could be ascertained only by sectioning. The first three instars, despite the apparent absence of tracheae in the second and third, must obviously obtain the necessary oxygen by cutaneous respiration, that is, through the skin, by a process of diffusion from the blood of the host, whilst the fourth obtains it in a more direct manner through the spiracles. The main point of interest in the respiration of *O. ilicis* is the absence of any sort of functional tracheal system in the second and third instar larvae. It might be argued that if a supply of oxygen in the tracheae was necessary in the first-stage larva, it would be even more necessary in the larger second and third instars. However, if we correlate respiration with activity we will see that this unusual method of development of the tracheal system is quite in keeping with the character of the larva. In the first stadium the larva has a pair of very large and powerful mandibles to wield, and this action when combined with other aggressive movements calls for a good deal of muscular activity, which, in turn, is dependent on an ample supply of oxygen—hence the presence of gas in the tracheae. (The nature of this gas has already been discussed by the present writer when dealing with the parasites of the pea moth (1939, pp. 295–6).) In the second and third instars there is no fighting to be done, and the only apparent activity, apart from some slight movement, is connected with digestion and allied functional processes. Since food is present in a highly assimilable form, a minimum amount of oxygen will be used up during the course of its conversion, and this low metabolic activity, when taken in conjunction with the extremely lethargic nature of these two stages, is sufficient to account for the absence of functional tracheae in the second and third instars.

The tracheal system of the mature larva is of the normal type and therefore no comments on its functioning are necessary.

(iv) *Arrested development in the Opiinae and some related forms*

The temporary cessation of growth which takes place in the larval development of *Opius ilicis* towards the end of the first stadium and the dependence of this parasite on certain changes in the host before further growth can take

place has been mentioned in Part V, but this phenomenon is so interesting and it offers such a marked contrast to the mode of development of *Chrysocharis gemma*, the other larval parasite of *Phytomyza ilicis*, that it is worthy of closer attention. The occurrence of a similar break in development in the following species: *Opius humilis*, *Diachasma Tryoni*, *D. fullawayi* (Pemberton & Willard, 1918); *Opius fletcheri* (Willard, 1920); *O. melleus* (Lathrop & Newton, 1933); and *Dacnusa areolaris* (Haviland, 1922), confirms the observations made on *Opius ilicis* and renders the subject still more interesting. All the parasites mentioned above, with the exception of the last named, which is a member of the closely related tribe Dacnusidae, are Opiines, so it is quite possible that further work on other members of the group will reveal arrested development to be a normal proceeding in this section of the Braconidae. A somewhat similar occurrence has been observed in the Ichneumonid—*Dioctes punctoria* (Thompson & Parker, 1928), a parasite of the European corn borer. This species overwinters in the corn-borer caterpillar as a primary larva, and further development does not take place until the spring, a method of hibernation which is totally different from that of the morphologically indistinguishable larva of *Eulimneria crassifemur*, another parasite of this host. The latter completes its metamorphosis in the late autumn and overwinters as a full-grown larva within its cocoon. Although similar in some respects, this arrest in development in *Dioctes* differs in at least three important particulars from that of *Opius ilicis* and its allies: (1) the Ichneumonid has a mature host at its disposal, whereas the larva in which *O. ilicis* lives continues to develop throughout the winter months; (2) in *Dioctes* there appears to be an absence of any dependence on the pupation of the host for the initiation of further growth in the spring, which is such a marked peculiarity of the Braconid; and (3) the phenomenon in the Ichneumonid cited, as in many other species with a similar habit of development, appears to be related solely to hibernation, which is definitely not the case in the Opiines. According to Dr W. R. Thompson, further examples of arrested development, of a type similar to that of *Dioctes*, are to be found in the Tachinidae, particularly in the Melanophorine parasites of woodlice, which, like *Dexia rustica* on *Melolontha melolontha* and *Masicera senilis* and *Zenillia roseanae* on *Pyrausta nubilalis*, hibernate in the host in stage II, and also in *Zygobothria nidicola* (Howard & Fiske, *Bull.* 91, p. 225), which overwinters in stage I, in the young caterpillars of the brown-tail moth.

In view of the fact that the Chalcid *Chrysocharis gemma* attacks the same stage of the holly leaf-miner as *Opius ilicis*, and like the latter is endoparasitic on this host, it will be interesting to compare the larval development of the two species. The first ecdysis does not take place in *Opius* until the host has pupated, but in *Chrysocharis*, on the other hand, larval development proceeds unhindered, and appears to be quite independent of the size or age of the host. As a result there is a good deal of variation in the size of the adult parasites which emerge from the leaf-miner larvae, much larger imagines being produced

from the mature hosts than from the younger stages. Haviland (1922) has observed similar variation in another Chalcid and has suggested that this diversity of size, owing to variability of nutrition, may lead to far-reaching results, such as for example, the production of new strains within a particular species. Keilin (1922) also commented on size variation in the Tachinid *Pollenia rudis*. He pointed out that the size of the imago was determined by the dimensions of its host, and stated that if the size difference should make mating impossible between large and small forms, distinct races might arise within the species. A good example of size variation in parasite adults has been observed in the Ichneumonid *Pimpla turionellae*. Three females, of which two were very much larger than the third, were reared by Mr A. L. Abel of this Laboratory, the two larger ones from the pupae of *Tortrix postvittana* and the smaller one from the puparium of *Actia pilipennis* (Tachnid), a parasite of this Tortricid. The first two were more than twice as large as the third—11 mm. in length (including ovipositor) compared with 4·5 mm. Mating between individuals of such diverse sizes would appear to be impossible, and as a result of this incompatibility three eventualities may be envisaged: (1) the small females mating with small males may produce a distinct race of small individuals parasitising the Tachinid larvae only; (2) the small imagines may be unable to find suitable mates and so die out (this is unlikely); or (3) the small females when mated may lay directly in *postvittana* larvae so that in the next generation normal individuals may again be produced and thus the occurrence of undersized individuals, being purely accidental, would not materially affect the history of the species, except in so far as it reduced its potential efficiency. Of these three possibilities, the first and the third are the most likely to occur. Of course, in the foregoing example the matter is a little more complicated, because of the hyperparasitic tendency of the Pimpline, but the main issue—the relation of size to nutrition—remains the same. Many more examples of size diversity could be brought forward, but this one must suffice. In the case of *Chrysocharis gemma* no special observations on the relation between age and size of host and the ultimate size of the adult parasites have been made, but the subject, given the necessary time, would be an interesting one. It is perfectly obvious, however, that although this Chalcid can develop on hosts of varying sizes and ages, the Braconid *Opius ilicis*, for some reason or other, is apparently unable to do so, and hosts in an advanced stage of development appear to be absolutely necessary for the completion of its metamorphosis. In discussing this problem, the most important point to bear in mind is the extremely close relation which exists between host pupation and the initiation of the second stage of growth in the parasite. How this latter is brought about may best be answered by suggesting that it is dependent on the production of certain chemical or physical changes in the composition of the host. That vast changes both of a chemical and physical character do take place at the time of pupation is well known, but the discovery of the exact nature of the exciting cause must await future

physiological experiments. Another question that is extremely difficult to answer, because of the very great, if not insurmountable obstacles lying in the path of experimentation on such small insects, is—what advantage has this particular mode of development for *Opius ilicis* and its allies? In reply, the following speculation may perhaps be permitted, but it must be clearly understood that it is only an expression of opinion for which, at the moment, because of the nature of the problem, there is no definite proof. It is possible that the main significance of arrested development in *O. ilicis* and related Braconid species is, that it is a method for ensuring the conservation of the food supply until it is sufficiently large to produce a normal-sized imago. Why this should be necessary in one species and not in another is not quite clear, unless it be that the metabolism of this parasite is of such a nature that the production of any adults, apart from stunted and probably useless individuals, demands the maximum amount of food for the proper development of the larvae. One beneficial result, which follows this developmental hiatus, is quite apparent, and that is, that the adults of *O. ilicis*, unlike those of *Chrysocharis gemma*, are all, more or less, uniform in size.

XI. Summary

1. While investigating the parasites of the holly leaf-miner (*Phytomyza ilicis* Curt.) with a view to utilizing them in the control of this troublesome pest of holly in western Canada, a species of *Opius*, which on examination proved to be new to science, was reared from the fly puparia.

2. A fairly complete account of the general systematics, distribution, biology, and morphology of the various developmental stages of this parasite is set down in the preceding pages. The primary larva is particularly interesting because of its unusual orientation. After the anatomical details had been worked out it was discovered that the concave side of the larva, which would normally be regarded as the ventral surface, is actually the dorsal one.

3. The genus *Opius*, whose distribution is world-wide, contains a very large number of species which parasitise important economic pests. In temperate regions the insects which suffer most from their attacks are species of *Pegomyia*, *Agromyza*, *Rhagoletis*, *Phytomyza* and *Cerodonta*, whilst in tropical and subtropical areas the most favoured hosts belong to one or other of the two genera *Dacus* and *Anastrepha*.

4. The host relationship of the genus, because of its importance from both economic and taxonomic standpoints, is discussed at some length.

5. In the first stadium *Opius ilicis* is a larval parasite, but the three succeeding instars live in the host pupa, and the imago emerges from the puparium. A very interesting phase in the life history of this parasite occurs towards the end of the first stage. At this point the development of the larva is arrested and further growth cannot take place until the host has pupated.

6. Very little work has so far been carried out on the larval morphology of the Opiinae, but that done up to the present, including the foregoing

descriptions, would seem to indicate that the larvae of this tribe form a fairly homogeneous group. The main distinguishing characters of these larvae are listed in Part VII.

7. It is pointed out that *O. ilicis*, in spite of being intrinsically inferior to *Chrysocharis gemma*, is responsible for the destruction of a certain number of hosts which escape the attentions of the latter parasite, and although the percentage accounted for is small (maximum parasitism in 1939 4%), it nevertheless fills a particular niche of its own, and so must be of some definite value in the scheme of control.

8. The chief method employed by the first instar of *Chrysocharis gemma* in the destruction of rival *Opius* larvae would appear to be direct mandibular attack. Several reasons have been put forward to account for the decided inferiority which is exhibited by the Braconid when it comes into conflict with this Chalcid.

9. In Part X, a number of interesting points which have a general bearing on the study of parasite larvae are discussed. These include the cephalic skeleton and its probable function in successive instars, the taxonomic value of this structure in the parasitic Hymenoptera, the apparent absence of a tracheal system in the second and third instar larvae of *O. ilicis*, and arrested development in the Opiinae and some related forms.

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EXPLANATION OF PLATE 1

Fig. 1. Holly leaf with incipient mine of *Phytomyza ilicis*. From mines of this size, which are present on the trees in December, the primary larva of *Opius ilicis* has been dissected out.

Fig. 2. Holly leaf with mature mine of *P. ilicis*. From this mine a pupal parasite, such as *O. ilicis*, has emerged.

Fig. 3. Underside of holly leaf showing two oviposition scars of *Phytomyza ilicis*. Through these scars, as suggested in the text, the females of *O. ilicis* might be able to parasitise the very young leaf-miner larvae.

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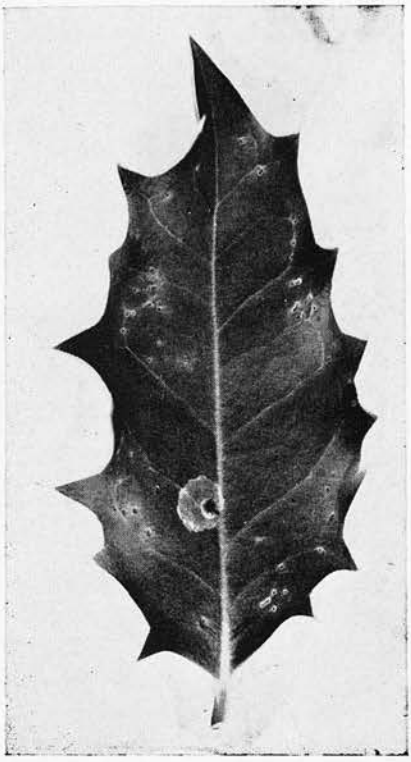

Fig. 1

Fig. 2

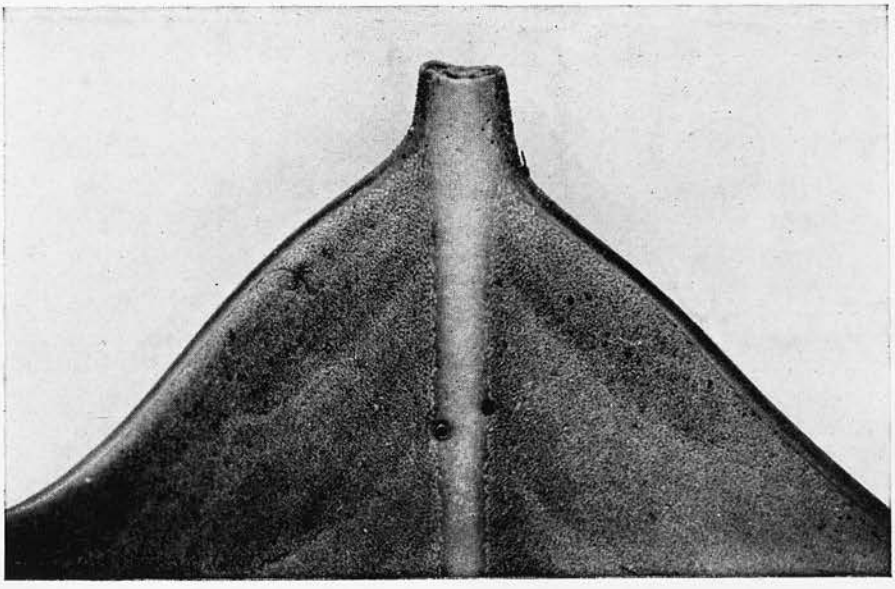

Fig. 3

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THE BIOLOGY OF *MICROPLECTRON FUSCIPENNIS*, ZETT. (CHALCID.), A PARASITE OF THE PINE SAWFLY (*DIPRION SERTIFER*, GEOFF.).

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(PLATE XVI.)

1. Introduction.

During the writers' work on the collection of parasites of sawflies of the genus *Diprion*, for introduction into Canada, a Chalcid, *Microplectron fuscipennis*, Zett. (family EULOPHIDAE), was found in considerable abundance parasitising *Diprion sertifer*, Geoff., in Austria, Hungary, and Jugoslavia. As this Chalcid readily attacked the cocoons of *Diprion polytomum*, Htg., the sawfly in Canada against which the introduction of parasites was directed, large numbers were collected in Hungary, and its biology, morphology, and artificial rearing were studied in some detail. An account of this will be given in the following paper.

2. Hosts, Distribution and Climate.

Microplectron fuscipennis appears to parasitise exclusively the genus *Diprion*, being recorded previously on seven occasions only, on *D. pini*, *D. sertifer*, and *D. pallidus*. (Zetterstedt records it under the name *Entedon fuscipennis*, Zett., as a parasite of Lepidopterous pupae from Lapland.) The writers have obtained it in considerable numbers from *D. sertifer*, on which it was mainly primary, but in a small proportion of cases it was apparently hyperparasitic upon a primary Cryptine parasite of *D. sertifer*, *Microcryptus basizonius*, Grav. In one infestation of *D. sertifer* in Hungary, where the parasitism was studied in detail, this Chalcid was

each cocoon most of the pupae and some larvae were unmistakably damaged and sucked dry, the rest dead and shrivelled. Although it would require breeding experiments to prove conclusively that *Eupelmella vesicularis* is hyperparasitic upon *Microplectron*, yet circumstantial evidence points strongly to this conclusion. Firstly, there is the fact that *Eupelmella* was invariably associated with *Microplectron* ; secondly, the fact that *Microplectron* had reached adult and pupal stages before being destroyed, indicating that *Eupelmella* laid in the cocoon after *Microplectron*, thereby exercising deliberate choice in such cases.

The geographical range of *Microplectron* is wide ; records come from Scandinavia (Zetterstedt, 1840 ; Thomson, 1876 ; Ruschka, 1924), Poland (Sitowski, 1925 ; Mokrzecki, 1927), Holland (De Fluiter, 1932), Germany (Hartig, 1837 ; Ratzeburg, 1844 ; Scheidter, 1934), and Austria (Schonwiese, 1934). During the present work it has been bred from *D. sertifer* in a number of localities in Austria, Hungary, and Jugoslavia, and specimens have been received from the same host from Sweden.

It is evidently capable of tolerating considerable diversity of climate. Professor Trägårdh writes that it is a very common parasite of *D. sertifer* in Sweden ; it is recorded by Sitowski as " common " on *D. pini* and *D. sertifer* in the vicinity of Posnen, and Mokrzecki mentions it as " especially numerous on both *D. pini* and *D. pallidus* " at Skierniewice, just south of Warsaw. All these are regions of rigorous climate, with long and hard winters and short, hot summers, but it seems to reach its maximum abundance in a warmer, more southerly climate. Thus, in the present work it has been found in Austria giving only 2–3 per cent. parasitism, in Hungary showing 10–15 per cent., and along the Adriatic coast-line of Jugoslavia reaching as much as 80 per cent., never less than 33 per cent. This abundance in Jugoslavia cannot be regarded as due to the direct influence of climate alone upon the Chalcid, but is the result of a whole complex of factors, at the root of which, indeed, is climate. The first, and direct, effect of the very long and hot summer in this locality is double ; a lengthening of the breeding season and a shortening of the life-cycle. Thus it was found, in the localities of maximum abundance, that all available cocoons of *D. sertifer* had been parasitised, and the majority of parasites had emerged by the beginning of August ; and since there are no other species of *Diprion* present and *D. sertifer* has but a single generation in the year and, so far as could be ascertained, *Microplectron* had no other hosts, its numbers must suffer severe reduction in late summer and autumn. This would leave a very small proportion of living parasites by the time new host cocoons are available at the end of the following May, yet between then and August it attains abundance. The rate of increase must, indeed, be amazingly rapid. In considering this sequence of events, it is rather surprising that *Microplectron* does not reduce both itself and its host to the point of extinction. The answer is that the host, *D. sertifer*, is maintained by a small proportion of cocoons that are in positions inaccessible to the parasite, usually because they are deeply buried in the soil ; in the case of the Chalcid a certain number of larvae go into diapause, even in this climate, in August, and these will not emerge until the following spring. These points are more fully treated in the next section on biology. A second and most important factor in bringing about the abundance in Jugoslavia is the presence of a very large supply of easily available host material. Along certain parts of the coast the sawfly is present every year in more or less large numbers (owing to the favourable climate) and spins its cocoons almost exclusively upon the tree-trunks, where they are readily accessible to the Chalcid. Cocoons spun on the ground are seldom deeply hidden, because of the scanty layer of pine-needles and hard rocky soil. The importance of a regularly abundant and easily available host in bringing about heavy parasitism by this Chalcid is emphasised by comparing these conditions with those obtaining in an infestation studied at Izsák in Hungary. The summer here is almost as long and quite as warm as that of the Jugoslavian coast, though considerably drier, and the winter is much colder. Infestations of *D. sertifer* here are sporadic, occurring for two or three years at long intervals and

onwards a number died daily, so that at the end of the second week the original number was reduced to half; at the end of the third week only one-fifth of the original population was alive, and at the end of the fourth week only one-sixteenth. The last female died on the thirty-second day after emergence.

There is always a very marked disproportion in the numbers of each sex emerging both in the field and in the laboratory, females being greatly in excess of males. The greatest difference was found in Hungary, where one male to six females was the average. In Jugoslavia the proportion was 1 : 4, and the same proportion was found in about a thousand individuals bred in the laboratory.

Mating takes place immediately after emergence. The very active male springs upon the back of the female and starts to caress her antennae, which are held erect, with his own, at the same time swinging his body backwards and forwards, raising and lowering his abdomen, and keeping up a rhythmic vibration of the wings the while. Occasionally he rests his body but keeps up the motion with his antennae. When the female is sufficiently excited she raises her abdomen, the male moves back and curves his abdomen round and under hers, in order to effect penetration and copulation. The whole process, including the preliminary courtship, occupies about a minute. Often a female will allow a male to mount her and caress her antennae, but will later resist any attempt at copulation.

Oviposition is effected through the sawfly cocoon on the prepupa. A female spends a long time on a cocoon, laying up to 20 or more eggs therein. In experiments, individual females laid, on the average, 45 eggs each, and the maximum number was 124 eggs for one individual. In conducting these experiments it was found that a certain percentage of females never laid any eggs (the cause of this is unknown) and these were eliminated from the computation. Unmated females oviposit freely and the eggs develop in the usual way, but result in an entirely male progeny.

The number of individual *Microplectron* emerging from a single cocoon was found to vary tremendously, from 5 to 119 in cocoons parasitised naturally in the field, and 120 is the highest number bred from a cocoon in the laboratory. The average number of individuals from a cocoon was found to vary according to locality; in Hungary it was 30·7, in Jugoslavia 72·5. Such large numbers undoubtedly result from the oviposition of several females in one cocoon, which would occur most commonly where the parasitism is highest. In such places superparasitism is also common. In one cocoon from Jugoslavia 164 eggs and 68 developing larvae of *Microplectron* were found.

As might be expected, a Chalcid with such powers of reproduction and such rapid development is capable of attaining a high degree of parasitism. The highest figure found was at Crkvenica on the Jugoslavian coast of the Adriatic, where 78 per cent. of *D. sertifer* cocoons held Chalcids; and at Senj, 20 miles south and still on the coast, 77 per cent. of cocoons. These figures cannot represent the full parasitism attained, as 15 per cent. and 12 per cent. of the cocoons in these two localities were destroyed by predators, which certainly show no discrimination in what they eat. At higher altitudes along this coast, from 300 metres upwards, the parasitism diminished in a marked degree, until at 600 metres only 33 per cent. was observed. This may be due, to a certain extent, to the slightly colder climate, but it is probably due mainly to the fact that at these altitudes the sawfly is less numerous and more sporadic in its outbreaks, large numbers being found, not every year, as on the coast, but only during epidemics occurring at longer intervals. One point has been mentioned before but may be stressed here again, as contributing to the high degree of parasitism found in Jugoslavia. This is the position in which the host cocoons are spun, mainly upon the tree-trunks, and when on the ground never deeply buried, owing to the lack of a thick needle or grass layer in the forest. This rendered them readily available to the Chalcid, which could reach the cocoons everywhere, though practically all the cocoons on the ground were subsequently destroyed by mice,

causing proportionately equal losses to hosts and parasites. In Hungary such parasitism was never found, 16 per cent. being the highest, at Cspel, close to Budapest, and an average of 10 per cent. at Izsák. One of the main reasons for this low rate was the inaccessible position of the cocoons generally in Hungary. Most of the pine forests here are on flat, sandy soil, with a thick covering of needles and sometimes grass. When such a covering exists *D. sertifer* spins its cocoons for preference on the forest floor, at any depth from superficially, on top of the needles, to two to three inches below the needle layer and just buried in the sand. Now this Chalcid apparently had not great powers of penetrating to these deeper layers, and the parasitism was always much greater in the case of surface cocoons than in those from the deeper layers, the difference being as much as 9 per cent. in extreme cases. This failure of the *Microplectron* to penetrate far into the needle layer meant that, in effect, only a small proportion of the cocoons, those at the top, was available for its oviposition. Another interesting observation made in this district showed that there was considerable local variation in this parasite's distribution within the infested area. In general, the parasitism was greatest where there was the greatest abundance of host cocoons, in the outlying and thinly infested areas it was comparatively scarce. Samples of 100 cocoons showed a variation in parasitism of 10 per cent. and 1 per cent. for different parts of the wood at the same time. It has already been mentioned that in Austria the parasitism by this species was low, approximately 2 per cent. at Unterwaltersdorf in the north, and about 3 per cent. in South Carinthia. The parasitism attained in Sweden has not been determined, and none of the writers quoted in the preceding section give any figures at all.

4. The Egg.

The eggs (fig. 4, *d*) are laid through the cocoon on the skin of the prepupa ; they adhere slightly to one another and are usually in groups of up to 20 or more. They are white in colour and sub-reniform in shape, tapering more acutely towards one end. The surface is shining and appears to be smooth under low magnification, but under high powers of the microscope it is seen to be covered with minute conical projections.

Length of egg, 0·34 mm. ; maximum breadth, 0·11 mm. At a temperature of 22°C. and 70 per cent. R.H. hatching takes place on the second or third day after oviposition.

5. Larval Instars.

There are five larval instars. The main points of difference between them are : size, the shape of the mandibles, the tracheal system and number of spiracles, and the number and size of the papillae. In the primary larva the mandibles are strongly curved, in the succeeding instars they are more or less straight. There are only four pairs of tracheae in the first-stage larva, in the mature, or fifth-stage, there are nine. The breadth of the head-capsule of each instar is as follows : 1st instar, 0·096 mm. ; 2nd, 0·128 mm. ; 3rd, 0·168 mm. ; 4th, 0·224 mm. ; 5th, 0·304 mm. These figures, providing a close and persistent ratio between the successive instars (1·33), gave a useful indication of the number of stadia, which was confirmed by mounts of each larval instar showing the newly-moulted head-capsule and parts of the skin of the preceding one. Each of the first four stadia occupies a period of one day, sometimes a few hours longer, and the 5th or final instar continues feeding for a further period of about four days after the 4th ecdysis. It then finishes feeding and becomes a resting larva, remaining in this stage for two to three days until it assumes a definite prepupal form.

6. Primary Larva.

The primary larva consists of a head and 13 clearly defined body segments ; the skin is transparent and glistening. It is somewhat fusiform in shape, being

broader anteriorly and tapering more towards the posterior extremity. The head is narrower than the first few segments. Length of primary larva, 0·35–0·38 mm.; maximum breadth, 0·11 mm.

The head is somewhat hemispherical in shape, and its chief features are a pair of antennae and a fairly well-developed internal skeletal system. The main function of this chitinised head skeleton (fig. 2) appears to be the support of the mandibles and the various mouth-structures associated with feeding. It also gives a certain amount of rigidity to the head. The mandibles, which are well developed and strongly arched, articulate on the superior and inferior mandibular struts. In the upper articulation the condyle is on the strut, while in the lower this order is reversed, the condyle being on the mandible. These mandibular struts or supports are joined together by the pleurostoma, while the inferior mandibular struts in this species are fused together to form a continuous rod underneath the mouth. The epistoma, an arch above the clypeus, arises from the superior or dorsal ends of the pleurostoma, while the hypostoma, consisting of a pair of long curved rods, is given off from the inferior or ventral ends. The hypostoma connects with the internal arched tentorium.

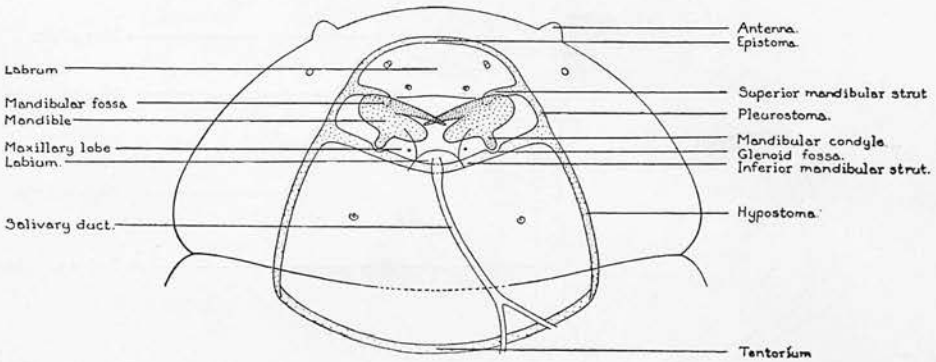

Fig. 2. Head of primary larva, showing head skeleton and various mouth appendages (× 350).

Of the non-chitinised mouth-parts, the labrum with two pairs of papillae, the maxillary lobes, each with a small papilla, and the labium are fairly well defined. The salivary duct, produced by the union of two internal tubes, is also clearly discernible. It opens into the mouth in the labial region. A pair of papillae are present in the labial region within the hypostoma, and another pair outside the supporting skeleton near the superior mandibular struts.

The tracheal system of the primary larva consists of two longitudinal trunks extending from segment 2 to 11. In segments 2, 4, 5, and 6 a lateral branch is given off from each trunk in the anterior portion of the segment to connect with an external spiracle, four pairs in all; while in segments 3 and 7–11 short, incipient branches are clearly defined. Anteriorly in segment 2 the two longitudinal trunks are joined by a transverse commisure, which gives off a pair of bifurcating branches to the first segment and the head-capsule. Posteriorly in segment 11 the longitudinal trunks are also transversely connected, and two branches project backwards into segments 12 and 13. From the point where the lateral and incipient lateral branches are given off a large number of very fine tracheae arise and ramify through the body of the larva.

7. Mature Larva.

The fifth-stage larva (fig. 4, *a*) consists of a head and 13 body segments, the segmentation being well, but not so clearly defined as in the primary larva. The main part of the body is orange-yellow in colour, but the head, first segment, part

of the second and last three or four segments are more or less transparent. It is cylindrical in shape, with a comparatively narrow head anteriorly, tapering posteriorly, and usually curved round ventrally, an aid to sticking on to its host. The last segment has a transverse indentation posteriorly.

The cuticle of the body is shiny and almost glabrous—only with a very high power of the microscope can a few small scattered papillae be seen. The head is hemispherical in shape and glassy-white in colour. It is divided into three lobes, a pair of dorso-anterior or epicranial, each bearing a conspicuous antenna, and an antero-ventral lobe below the mouth.

The average length of the fully extended larva is 3·36 mm. and its maximum breadth 0·86 mm.

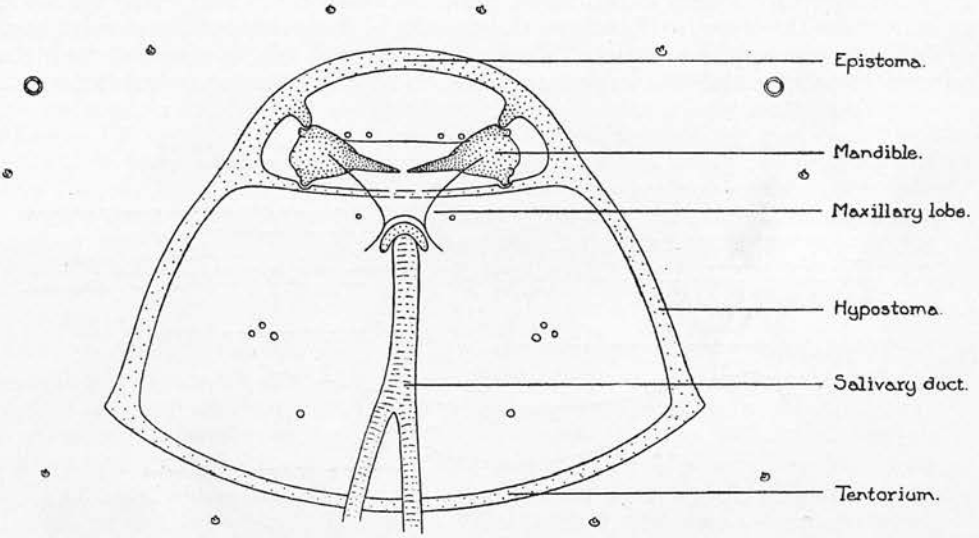

Fig. 3. Head of mature larva, showing head skeleton and various mouth appendages (× about 187).

The skeleton of the head (fig. 3) resembles that of the primary larva—epistoma, pleurostoma, superior and inferior mandibular struts, hypostoma, and tentorium all being present. In this instar the rod formed by the fused inferior mandibular struts is not so clearly defined as in the primary larva, and the mandibles are also different. Instead of being strongly arched, they are now almost straight and supported on strong triangular bases. The annulated salivary duct formed from the fusion of two internal ducts is a prominent structure. Near the point where it enters the mouth in the labial region it is partly surrounded by an inverted U-shaped chitinous rod. A number of papillae are present—one very large and marked pair outside the supporting skeleton in a line (one on each side) with the superior mandibular articulation. There are also three pairs of smaller papillae in this region. A further two pairs are situated on the skin underneath the region of the tentorial-hypostomal connection. On the area within the supporting skeleton the following papillae are present : two pairs on the labrum, a pair on the maxillary lobes, two sets of three on the sub-labial region, and a final pair below this latter group. The antennae, when viewed from above, are seen to have two small papillae on their upper surface.

There are nine pairs of spiracles present (fig. 4, *e*) in segments 2–10, and the general tracheal system of longitudinal tubes and branches is similar to that described for the primary larva.

8. Prepupa.

The cessation of feeding by the mature larva marks the beginning of the prepupal stage. For two or three days it remains unchanged in appearance and then becomes clearly demarked into three new regions (fig. 4, *b*), destined to be the head, thorax, and abdomen of the pupa. The head region is composed of the old larval head and first segment. Behind this a slight constriction appears separating it from the two thoracic segments now much enlarged, which are themselves separated from the abdomen by a similar constriction. Defaecation usually coincides with this change, and as a result the prepupa assumes a white colour. Twenty-four to 30 hours after this change the prepupa moults and enters the pupal stage.

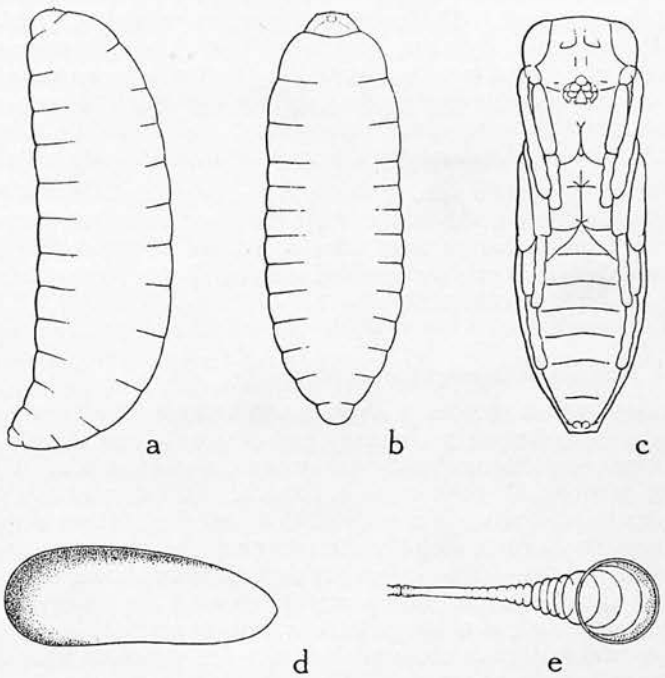

Fig. 4. *Microplectron fuscipennis ; a*, mature larva ; *b*, prepupa ; *c*, pupa (all × 10) ; *d*, egg (× 60) ; *e*, spiracle of mature larva (× 300).

9. The Pupa.

In the newly formed pupa (fig. 4, *c*), which is white in colour, both wing and leg rudiments can be clearly seen glued to the body. The eyes, mouth-appendages, thoracic and abdominal segmentation are also fairly well defined. After some hours the white colour changes to deep orange, and black pigment is deposited on the abdomen both dorsally and ventrally, and to a less extent on the thorax dorsally. In a day or two the whole of the pupa darkens, although the former ground-colour of deep orange is still discernible, particularly in the intersegmental areas. More pigment is gradually deposited until the pupa becomes quite black.

The average length of the pupal stage is 7–8 days.

10. Rearing in the Laboratory.

Since *Microplectron* has never been found naturally parasitising cocoons of *Diprion polytomum*, the whole success of the introduction depended upon its willingness to do so. This was tested in the laboratory, and in order to make the

tests more significant, cocoons of *D. polytomum* from Canada were used throughout the experiments. Owing to its readiness to mate and oviposit, the fairly high number of eggs per female, and the short life-cycle, it was easy to maintain a large stock of the parasite in captivity.

Rearing was carried out on a small scale in glass cylinders, $4\frac{1}{2}$ in. by $3\frac{1}{2}$ in., having the top covered with muslin secured by a rubber band, and the bottom resting on filter paper inside the cover of a petri dish. Water was supplied from damp cotton wool covered with muslin in a glass receptacle, and food by a lump of sugar and a raisin. Up to 100 females with males were placed in each cage. Cocoons of *Diprion polytomum*, gummed on a strip of paper, were then introduced into the cylinders and the latter placed on shelves in the room window, where the maximum amount of light could be obtained. The room temperature was 18°C. and the relative humidity 40–45 per cent. For the first day or two after emergence the females were rather slow in ovipositing, but from the third day onwards egg-laying was rapid. Fresh cocoons were placed in the cages two or three times a week and the old ones transferred to the constant temperature and humidity room (22°C. and 70 per cent. R.H.), where the complete life-cycle occupied a period of about 3 weeks.

In mass breeding large bell jars, 12 in. by 8 in., were used. These were prepared in the same way as the smaller cages, with the exception that the cocoons were gummed on cardboard strips on four sides of a piece of wood (Plate xvi). Such jars held large numbers of adults and enabled us to carry on a large rearing programme with a minimum amount of attention.

11. Value as a Parasite of Diprion polytomum, Htg.

In view of the fact that cocoons of *Diprion sertifer* containing nearly eight millions of this parasite were collected in Hungary and despatched to Canada during 1934, it is not out of place to discuss briefly the prospects of *Microplectron* as a parasite and controlling agent of *D. polytomum* in Canada. Criticism of the whole project might be well made here, when it is realised that this Chalcid has never been found on *D. polytomum* in Europe, despite their having the same geographical range. A knowledge of the status of the Spruce Sawfly in Europe, however, affords a ready explanation and allays such doubts as might be felt. In Europe *D. polytomum*, though widely distributed, is a comparatively rare insect. It has solitary larvae, and its cocoons are scattered and well hidden. Its numbers vary tremendously from year to year and from place to place; an infestation has only once been recorded, and then it was of negligible extent and disappeared in two years. Thus, the most important conditions reproduced by *D. sertifer*, abundance and regular appearance, are entirely lacking in *D. polytomum* in Europe, and the absence of this parasite is at once understood. In Canada, as will be pointed out, the status of the latter sawfly is entirely different.

The first and essential point, that this parasite will oviposit readily in cocoons of the Canadian *D. polytomum*, has been amply proved in the laboratory, both at Farnham House and in Canada. All the experiments at Farnham House have been performed with cocoons sent over from Canada, and the success of this rearing fully demonstrates the attraction and suitability of this host for *Microplectron*. Any final doubts must be swept away by the news, just received, of the recovery of this parasite from *D. polytomum* cocoons in at least three localities in Canada, where liberations were made only last summer.

Equally important is the suitability of the Canadian climate for the establishment and increase of this Chalcid. If one may judge from its geographical range in Europe, there should be no question as to its establishing itself in Canada, at least in the lower regions of New Brunswick and Quebec, where the temperature range is not very different from that of South Sweden or Central Poland. Its establishment

in the high regions of the Gaspé Peninsula, the site of the original infestation of *D. polytomum*, will depend largely on its ability to withstand a low temperature for five or six months of the year, the winter here being both longer and considerably colder than in the parts of Europe mentioned. Actually this, in itself, should not be detrimental to the parasite, as the cocoons in which it overwinters will be buried deeply in snow, but owing to the shorter summer and lower temperatures (considerably below those of Sweden or Poland) the breeding period in the Gaspé will be very much curtailed and the rate of development rather slower. The places where it is likely to be most successful will be the lower country of New Brunswick, round the coast-line, and along the shores of the St. Lawrence. As it is common right down to the shore along the Adriatic coast, it has the advantage of being able to flourish in a maritime climate, with a considerable amount of salt in the air.

The regular abundance of the host experienced in the infested area in Canada is a most decided advantage. The fact that a large proportion of the sawfly prepupae, normally overwintering in the cocoon, remain in diapause for one or two years, ensures an ample supply of cocoons throughout the summer, on which the parasite might pass through successive generations as long as the weather is favourable. This is probably one of the most influential factors in enabling it to attain a high degree of parasitism.

The position of the host cocoons, as we have seen, is also of great importance. In Canada the majority of the cocoons are spun upon the forest floor. If this has a thick layer of needles and moss, parasites will be adversely affected, but if the needle layer be thin, or cocoons occur upon trunks or branches (for example in warmer localities where the host is bivoltine) it will have full scope for its activities.

The fecundity of this species is its greatest asset. Its rate of increase is tremendous, a female laying from 50 to 100 eggs in six or seven days. This is discounted somewhat by the invariable habit of multiple oviposition, from 10 to 50 or more eggs are laid in the same cocoon, so that the parasitism is not spread out to the best advantage. Nevertheless, the rate of increase is not diminished, as all the eggs usually hatch and develop successfully, 120 imagines having been reared from a single cocoon. Besides being a rapid and reproductive breeder, it will breed under almost any conditions, copulation and oviposition following immediately upon emergence and the full complement of eggs being laid generally within a week, so that the presence of food and moisture, though undoubtedly prolonging life and increasing fecundity, are by no means essential. For this reason mass production of the parasite in the laboratory is comparatively simple. This again is a point in its favour, as by mass breeding and by obtaining large numbers of heavily parasitised cocoons from Jugoslavia it would be possible to make really adequate liberations at a great many points in the infested area, a most essential proceeding in dealing with an outbreak of such colossal extent as that of *D. polytomum* in Canada.

It will thus be seen that we have in *Microplectron fuscipennis* a hardy parasite possessed of that most essential quality, a rate of increase considerably more rapid than that of its host; and, furthermore, that in Canada are reproduced, except for climate, those conditions prevailing in Jugoslavia—an absence of alternate hosts and a regular and abundant supply of *Diprion*. Moreover, this supply of hosts undergoes, at present, none of that seasonal reduction brought about by the parasite itself in Europe.

12. Summary.

Cocoons of *Diprion sertifer*, Geoffr., containing nearly eight millions *Microplectron fuscipennis*, Zett., were collected in Europe in 1934 and despatched to Canada for the control of the Spruce Sawfly, *Diprion polytomum*, Htg.

This parasite is widely distributed throughout Europe as a primary parasite of several species of pine sawflies of the genus *Diprion*.

A full account of the biology and a detailed description of the various stages is given.

In the laboratory it was reared in large numbers on the cocoons of *D. polytomum* from Canada.

Its chances of success in Canada depend on its acclimatisation and the accessibility and quantity of host material. Its tremendous fecundity and rapid rate of increase are greatly in its favour.

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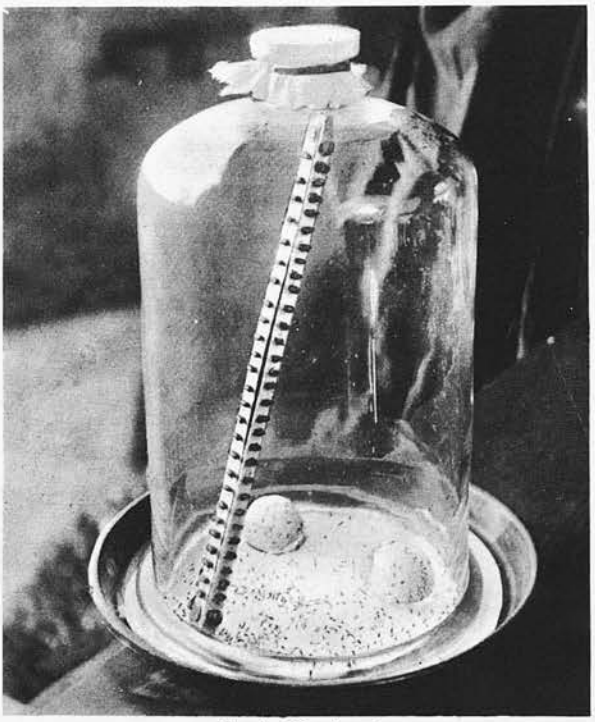

Fig. 1. Rearing jar.

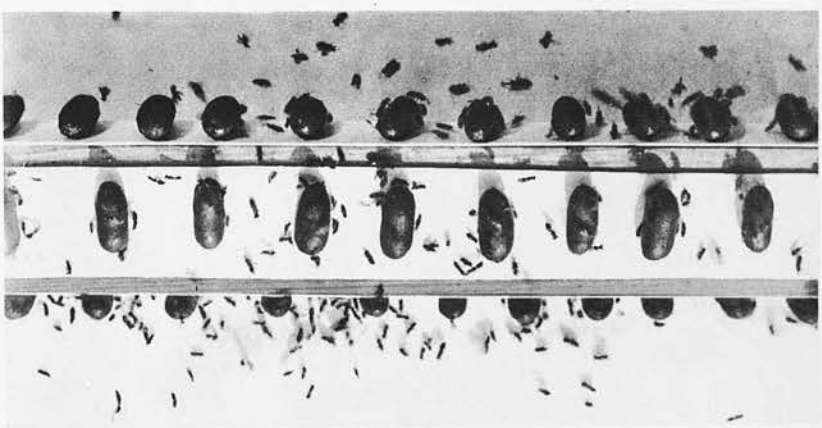

Fig. 2. Enlargement of cocoon strip, showing adults ovipositing.

Fig. 3. Opened cocoon showing mature larvae.

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V.

THE INSECT PARASITES OF THE SPRUCE SAWFLY (*DIPRION POLYTOMUM*, HTG.) IN EUROPE.

BY

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Farnham House Laboratory, Imperial Institute of Entomology.

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CONTENTS.

Introduction.

In 1930 a severe outbreak of the Spruce Sawfly, *Diprion* (*Lophyrus*) *polytomum*, Htg. (*hercyniae*, Htg.), was discovered over a large area in the centre of the Gaspé Peninsula in eastern Quebec, Canada. The insect was doing very severe damage to valuable stands of Black and White Spruce (*Picea mariana* and *P. canadensis*) through defoliation of the trees by its larvae. In the following year it had increased considerably and it was estimated that 2,000 square miles of forest were badly damaged. By 1933 the area of severe damage had increased to 4,000 square miles. The sawfly continued to spread at this alarming rate until in 1936 the area of severe damage covered approximately 10,000 square miles and the range of the insect had extended southward through the United States into Connecticut (specimens have been captured not far from New York), westward as far as Lake Temiskaming in Ontario, and northward across the St. Lawrence River to Lake St. John. It now constitutes one of the most serious and dangerous forest pests ever introduced into North America.

D. polytomum is a native of Europe, where it has an extremely wide distribution, being found over the whole range of Spruce (*Picea excelsa*) from Finland to Jugoslavia, but where it never causes any serious damage to the forests, being, on the whole, a comparatively rare insect, except under certain favourable sets of conditions. Under the most favourable conditions, however, it never attains anything approaching the abundance of any of the common European forest pests. The reason for this tremendous and rapid increase in Canada is probably twofold. Firstly, the sawfly is reproducing parthenogenetically in Canada, males being almost unknown, whereas in Europe it is normally bisexual with the sexes in general in approximately equal proportions. The effect of this is virtually to double the reproductive rate in Canada. Secondly, as is usually the case with accidentally imported insects, the sawfly arrived in Canada without any of its natural enemies and up to the present no native parasites have been found attacking it in its new environment. This state of affairs led to a request, in 1932, from the Canadian Government to Farnham House Laboratory, for a study to be made of *D. polytomum* in Europe with the object of collecting and sending such of its natural enemies, especially insects, as might be considered of possible value in helping to check the spread and ultimately reduce the infestations in Canada.

The work commenced at once, and by the autumn of 1932 a large part of Saxony and Bohemia had been searched for the sawfly, five different collecting points had been located and between five and six thousand larvae and cocoons collected. A number of these were used for studying the insect parasites, but 3,267 cocoons were sent to Canada that winter. The results of this and subsequent years' investigations showed that many of the major parasites of *D. polytomum* occur also on other species of the genus *Diprion*, which frequently appear in great numbers in Europe. Laboratory tests at Farnham House and field tests in Canada showed that the parasites from other hosts will usually attack the Spruce Sawfly, so from this time on, although the main efforts were always concentrated on the collection of *D. polytomum*, outbreaks of other species showing suitable parasitism were always sought. In this way it was possible to make very large collections of some parasites, which could never have been obtained in any quantities from the never numerous Spruce Sawfly. In 1932, 5,202 cocoons of *D. polytomum* and 1,550 heavily parasitised cocoons from a mixed infestation of *D. sertifer*, *D. frutetorum*, and *D. virens* were sent to Canada. In the succeeding years there was a tremendous increase in the collections of both *D. polytomum* and other species, partly through increased efficiency because of experience gained and getting to know the people and countries in Central Europe, but mainly through the increased funds made available by the Canadian Government. With this extra money it was possible to get together and train a team of men for collecting *D. polytomum* in Czechoslovakia, where, for several reasons, all the

collections of this species have been made. In 1934 only four such men were employed, but by 1936 nearly 30 men had been trained and over 20 were working in the field at once. This enabled the Entomologists from Farnham House, who had previously been fully occupied with collecting, to devote more time to the scientific side of the work and to locating and collecting material of other hosts from other countries. Actually in 1936, the chief of the team of collectors, a very able Russian, Dr. L. Černosvitov, was left in charge of the collecting of *D. polytomum* for most of the summer and only one Entomologist went out from England, whereas hitherto it had always been necessary to employ two on this work. The search for outbreaks of other species of *Diprion* has led from Sweden to the Adriatic coast, and the main collections, in all cases of *D. sertifer*, have been made in Hungary, Czechoslovakia and Sweden. The numbers of cocoons collected and despatched from Europe during the last three years is given below. Most of this material has been sent on to Canada from Farnham House, only small samples having been retained for study.

Year	*D. polytomum* cocoons	*Diprion* spp. (mainly *sertifer*)	Eggs of *D. sertifer*
1934	15,364	4,405,179	—
1935	55,716	1,713,750	391,160
1936	202,267	20,858,241	161,950

With the 1932 and 1933 shipments this makes a total of 281,916 *D. polytomum* and 27,531,830 *D. sertifer*, etc., together amounting to 27,813,746 cocoons and eggs, containing from 25 per cent. to 80 per cent. parasites.

This work is still being continued, but it is considered advisable at this point to summarise and put on record some of the immense amount of data and information gleaned on such an undertaking. The present paper has a purely practical aim, of recording all the insect parasites found attacking *D. polytomum* in that part of Europe where our work lay, to give brief but sufficient descriptions to facilitate the recognition of the adult forms by the practical worker, and in the case of all the primary parasites to give, so far as we are able, some account of their biology and descriptions of the larval stages sufficient for recognition. Finally, notes are added for each species, giving our own opinion as to its suitability or not for introduction into Canada and its prospects of success.

The constant travelling in many countries of Europe which this work has involved has brought us into contact with a great number of people, both scientists and others, and has left us with many very good friends. To all these friends we are indebted for their invariable courtesy and help, which has done so much to make our work both pleasant and successful. We should like to express our gratitude more especially to Professor Julian Komárek and his staff, particularly Dr. Anton Pfeffer, of the Forest Protection Institute in Prague, where for five years we have had our headquarters; to Professor Ivar Trägårdh and his staff of the Skogsförsöksanstalt in Sweden, for his help in making big collections of *D. sertifer* cocoons and eggs in 1935 and 1936; to Professor Bako and his staff of the Növényvédelmi Kutátó Intézet in Budapest, our biggest collections of *D. sertifer* having come from Hungary in 1934, 1935, and 1936; and to Professor Heinrich Prell of Tharandt Forstliche Hochschule, where our first investigations on *D. polytomum* were successfully started.

2. Previous Records of Parasites.

Previous to the present work only 12 species of parasites had been recorded from *D. polytomum*. These records gave no exact data as to the life-histories or interrelationships of the parasites, and frequently it was not even stated whether they were primary or secondary upon this host. Only the commonest species had been

studied in any detail, and then only in their occurrence on other hosts, such as *Exenterus marginatorius* on *Diprion pini* and *D. sertifer*, and *Sturmia inconspicua* on certain Lepidoptera. In the light of our present investigations we cannot accept even this information as invariably correct ; for example, Sitowski (1925) states that *Exenterus marginatorius* lays its eggs *in* the body of *D. sertifer* and that development is internal. The following is the list of the previously recorded parasites of *D. polytomum* :—

HYMENOPTERA :

ICHNEUMONIDAE :

Cryptinae : *Habrocryptus* (*Caenocryptus*) *polytomi*, Tschek (De Gaulle, 1908).

Ophioninae : *Holocremnus ratzeburgi*, Tschek (Schmiedeknecht, 1908 ; Forsius, 1932).

Tryphoninae : *Exenterus tricolor*, Roman (Forsius, 1932).
Exenterus marginatorius, F. (Forsius, 1932).
Lamachus spectabilis, Holmgr. (Forsius, 1932).
Mesoleius vepretorum, Grav. (Giraud, 1877).
Mesoleius multicolor, Grav. (De Gaulle, 1908).
Mesoleius multicolor var. *dives*, Holmgr. (Giraud, 1877).
Tryphon laevis, Ratz. (André, 1879–81).

DIPTERA :

TACHINIDAE : *Diplostichus janithrix*, Htg. (Baer, 1920).
Ptychomyia selecta, Mg. (Baer, 1920).
Sturmia inconspicua, Mg. (*bimaculata*, Htg.) (Baer, 1920).

3. Parasites met with in the Course of the present Work.

The following 31 species of parasites have been bred from larvae or cocoons of *D. polytomum* during the present work, the majority of the host material having been collected in Czechoslovakia, a small quantity only coming from Saxony, Bavaria, and Austria. It will be observed that half of the parasites previously recorded do not appear here. We are inclined to explain this, in the case of the three species of *Mesoleius* and *Tryphon laevis*, by pointing out that these are very old records and the validity of the identifications can by no means be relied on ; indeed, all our work with the systematics has shown the inadvisability of relying on identifications in previous parasite records. In the case of *Diplostichus janithrix* and *Ptychomyia selecta*, which are recent and certainly reliable records, it is quite likely that our present area of activities has not come within the distribution of these Tachinids.

HYMENOPTERA :

ICHNEUMONIDAE :

		Stage of host attacked.
Cryptinae :	*Microcryptus basizonius* var. *curtulus*, Kr.	Prepupa in cocoon.
	Leptocryptus aereus, Grav.	Hyperparasite.
	Spilocryptus abbreviator, F.	Prepupa in cocoon.
	Spilocryptus abbreviator, var. *hopei*, Grav.	Prepupa in cocoon.

Cryptinae :—*continued.*		
	Habrocryptus polytomi, Tsch.	Prepupa in cocoon.
	Hemiteles areator, Panz.	Prepupa or hyperparasite.
	Hemiteles sordipes, Grav.	Hyperparasite.
	Gelis (*Pezomachus*) *acarorum*, L. ...	Hyperparasite.
	Gelis sp.	Hyperparasite.
Pimplinae :	*Delomerista* sp.	Prepupa or pupa in cocoon.
	Pimpla alternans, Grav.	Prepupa or pupa in cocoon.
Ophioninae :	*Mesochorus thoracicus*, Grav.	Hyperparasite on larval parasites.
	Mesochorus fulgurans, Curt.	Hyperparasite on larval parasites.
	Mesochorus (?) *dimidiatus*, Hlmgr. ...	Hyperparasite on larval parasites.
	Holocremnus ratzeburgi, Tschek ...	Larva.
Tryphoninae :	*Lamachus* sp.	Larva.
	Lamachus spectabilis, Hlmgr. ...	Larva.
	Exenterus tricolor, Roman	Larva or prepupa before spinning.
	Exenterus adspersus, Hart.	Larva or prepupa before spinning.
	Exenterus marginatorius, F.	Larva or prepupa before spinning.
	Exenterus sp. (near *adspersus*) ...	Larva or prepupa before spinning.
BRACONIDAE :		
Braconinae :	*Microbracon* sp.	?
CHALCIDIDAE :		
Toryminae :	*Monodontomerus dentipes*, Dalm. ...	Prepupa in cocoon, rarely hyperparasite.
Pteromalinae :	*Habrocytus* sp.	Hyperparasite.
	Eutelus subfumatus, Ratz.	Prepupa in cocoon.
	Dibrachys cavus, Walk.	Prepupa or hyperparasite.
	Diglochys lophyrorum, Ruschka ...	Prepupa or hyperparasite.
	(?) *Stenomalus* sp.	?
Eulophinae :	*Pleurotropis* sp.	Hyperparasite.
	Microplectron fuscipennis, Zett. ...	Prepupa in cocoon, rarely hyperparasite.
DIPTERA :		
TACHINIDAE ...	*Sturmia inconspicua*, Mg.	Larva.

It is interesting that of the 20 parasites that can act in a primary capacity, at least 5, or one quarter of the number, can also be hyperparasitic. It is especially interesting to see species such as *H. areator* and *D. cavus* acting as primaries.

Thus only 15 species are obligatory primaries and 9 obligatory secondaries. This is undoubtedly due to the host being a Hymenopteron, and certain of the more polyphagous species are ready to victimise the sawfly or its parasites with equal facility. In some cases, however, notably *Microplectron* and *Monodontomerus*, hyperparasitism is the result rather of accident than deliberation, oviposition by these species taking place in a cocoon already containing an immature grub or egg of a primary Ichneumonid parasite. The more quickly developing Chalcids overtake the larger Ichneumonid and finally consume it as well as the true host.

In two cases (*Microbracon* and *Stenomalus*) only a single, rather doubtful individual was obtained and the status is unknown. Nearly two-thirds of the parasites (19 species) attack the host in the cocoon, only 11 species attacking the larvae. Twelve of the primary or facultative primary parasites attack the cocoons and 8 attack larvae. As might be expected, most of the secondaries oviposit in the cocoons, but the three species of *Mesochorus* oviposit in already parasitized larvae. The parasites are dealt with separately in the following section, and their inter-relations with the host and with one another are being dealt with more fully in a later paper.

4. Practical Notes.

Before proceeding with the descriptions of the individual parasites, it is necessary to give some general notes which must be borne in mind when reading the descriptions, also some practical advice as to the preparation of the larvae for examination. This latter is given not only as information, but also in order that the method of preparation of the specimens on which the descriptions and drawings are based may be known. This is important, since preparations can assume very different appearances according to the methods employed.

In no case has a full description of the adult insects been attempted, merely sufficient being given to enable the recognition of the various species among the *D. polytomum* parasites or in their own genera. This is intended mainly for the practical worker in the field, who has not access to a full library. The adult descriptions (and the key) refer always to the females unless explicitly stated. Usually the male is very similar in general coloration and characters, differing only in size and the shape of the abdomen. Wide differences in the sexes are mentioned. The length of the adult is taken from specimens bred from *D. polytomum* and does not include antennae or ovipositor. The size is apt to vary considerably, in the case of the Ichneumonids depending on the size of the host, in which the males are much smaller than the females ; and in the case of the Chalcids depending also on the number of individuals reared from each host.

In dealing with the larvae size is found of little value for recognition for the same reasons, consequently the dimensions of the full-grown larvae are rarely given. The chitinized mouth-parts and tentorium of the larval head afford the best and most easily recognisable characters, these being quite easily seen in the living larva with a hand lens or binocular microscope. The separation of allied tribes and genera, however, usually entails rather finer points of distinction in the mouth-parts and skin structure, and spiracles also. For this, examination of a preparation under the compound microscope is necessary. All the drawings and descriptions have been made from such preparations. It is inevitable that the larval head will be more or less flattened in mounting, and therefore the general appearance of the mouth-parts and tentorium will be somewhat altered, having a rather broader lay-out than in the living larva. The angle at which the head lies on the slide also makes a considerable difference to the appearance. The size, shape, pigmentation and proportions of the different structures, however, remain unaltered. The method of preparation for all our specimens has been identical and therefore the figures are comparable. The method is given below. For description and illustration the spiracles are always taken from the thoracic region of the larvae, although there is not much variation

over different parts of the body in the Ichneumonids. The illustrations represent, as near as we can get, the appearance under high magnification, without being diagrammatic or in true optical section. Skin structure is always taken from the mid-ventral area of the first thoracic segment so as to be strictly comparable. Occasionally the skin structure varies over the different segments, and usually in this region it is most developed. Also, some parts of the skin of this region is usually present when the head of the larva is mounted alone.

Since this paper is written mainly from a practical point of view, the life-history and description of the larval stages is given only for the primary parasites of *D. polytomum*. The hyperparasites can all be grouped together as of no value for the project in its present stage. They are easily distinguished from the primary parasites on a careful inspection of the cocoon in which they developed. The larvae of all the primary Ichneumonid parasites, with the exception of *Delomerista* and *Pimpla*, on reaching maturity spin a thin, flimsy cocoon of one or more layers of white or grey papery material, within the host cocoon, the remains of the sawfly prepupa being excluded. If then any larvae are found feeding on anything *inside* this white papery cocoon it is certain they are secondary, this being especially obvious in the case of Chalcids. If the secondaries have reached maturity they spin a second papery cocoon (except the Chalcids), usually excluding that of the primary on which they have fed. Besides this, the remains of the primary larvae can always be found, though sometimes not very easily. If the primary had not reached maturity when it was killed, of course no cocoon will be present, but in this case its remains, together with those of the sawfly prepupa, can always be found on careful search.

In quoting percentages of parasitism for different species on *D. polytomum*, figures are given only when samples of over a hundred specimens, usually considerably more, have been examined. Figures for larval parasites are obtained either from the dissection of the host prepupae or from emergences from cocoons that were spun in captivity, so that there was no loss from competition with the intrinsically superior cocoon parasites or hyperparasites. Figures for cocoon parasites are from emergences from cocoons collected in the field. This is inevitably a less reliable figure than that for larval parasites, always underestimating the true rôle played by the cocoon parasites. As will be pointed out, these usually have more generations in the year than the host, especially the Chalcids, adults being usually present in the field throughout the summer months, owing to overlapping of generations and delayed emergences, so that oviposition on the host cocoons is continually going on. Thus the parasitism will depend entirely on when the samples are collected. Even if the collection is made as late as possible, just before the emergence of the adults, so as to get maximum exposure to parasitism, this will not include some individuals, especially Chalcids with a very quick development, which have already emerged. Thus the figures quoted in the case of the cocoon parasites are the very minimum and by no means represent the full losses inflicted on the host by these factors.

In taking autumn or winter samples of cocoons it is often found tedious or inconvenient to wait until the following spring for emergences. If the cocoons are collected in autumn and placed straight into a warm atmosphere this will in no way accelerate development, emergence taking place, as in naturally situated cocoons, in the following spring, or at most a few weeks earlier. If, however, the cocoons are collected late in winter and then brought into a warmed room, emergence usually takes place considerably earlier. Working on the assumption that exposure to a low temperature for a certain period is necessary for the development of the overwintering parasite eggs or larvae, we have evolved the following simple method of forcing emergence. Cocoons collected or bred in autumn are slowly cooled down to a temperature just above freezing, 1 or 2°C., at which they are held for a month, and then slowly brought to successively higher temperatures until about 26°C. is reached. This so accelerates development that adult parasites and sawflies may be obtained

by Christmas, three or four months before the normal time of emergence. The lowering and raising of the temperature must be gradual, lasting over three or four weeks, and the humidity should be kept above 60 per cent. R.H., and care taken not to allow it to increase too much during the cooling process. If the cocoons are treated *en masse*, cardboard or wooden boxes are better containers than metal boxes, as they do not encourage the condensation of moisture. Glass-top boxes are very bad ; gauze-topped boxes are better. For small quantities probably the best containers are short lengths of wide glass tube, plugged at each end with cotton wool. For individual cocoons we always used gelatine capsules. These cannot be subjected to a very high humidity however, for at 70 per cent. R.H. they go soft.

Preparations of parasite larvae can be made either from living larvae themselves, which is vastly easier and preferable, or from the cast skins of mature larvae found in the cocoons from which the parasites have emerged. This latter method was used in every case at the beginning of the work, in order to recognise the larval stages of the different parasites. Preparations from living larvae are best made by keeping the killed larva either in water or in a stoppered glass tube for two to three weeks until the body contents have completely decomposed. Then, on opening the larva, the inside is easily washed away under gently moving water, and the chitinous skin and head structures will be in perfect, undamaged condition. For mounting the whole preparation a mid-dorsal incision should be made the length of the whole body from the tail to the back of the head, then lateral incisions round the base of the head, separating it from the first segment, to which it should remain attached only in the ventral region. In this way the skin can be spread out flat, displaying the spiracles, tracheae and other structures, and the head will assume a position with the chitinous mouth-parts, struts, and arches slightly flattened into a plane more or less parallel with the slide. Alternatively, the head can be cut completely off round the junction with the first segment and mounted separately from the skin. A far quicker method of preparing fresh larvae is to make the dorsal incision and remove most of the body contents first, or cut off the head, and just bring to the boil in a 5 per cent. solution of caustic potash. It should not be boiled for any time or the fine chitinous structures will be lost. If not boiled enough the flesh is difficult to remove. After potash, wash and remove the remaining flesh and muscles with a fine brush or needle. In order to prepare a parasite skin from the cocoon remains, the whole contents of the sawfly cocoon should be placed in a watch glass, the papery cocoon of the parasite removed and the remainder allowed to soak in water for a short while. The last larval skin of the parasite is usually found attached to the little blob of excrement at one end of the parasite cocoon, or mixed up with the cast pupal skin. When removed it is usually found full of bubbles, especially the head-capsule, the most important part. The best way of getting rid of these is by boiling in water. The skin is then soft enough to be carefully stretched out and mounted.

In our experience, by far the best mounting medium is de Faure's solution or Keilin's mixture, into which the preparation can be placed direct from water. If sufficient medium is used the coverslip need not be supported. If desired, it can be supported on tiny pellets of plasticine. This is largely a matter of choice. After the cover-slips are in position, it is important so to manoeuvre the head, by gentle pressure, that the plane in which most of the mouth structures lie is parallel to the slide, otherwise a very distorted and misleading view will be obtained. In these low refractive index media the chitinous structures, even the tiniest hairs and sensillae, show up to the best advantage. We now use exclusively this method of mounting for all preparations of the immature stages, eggs or larvae, finding it gives the best results as well as being the easiest. It can be employed in the field, the slides, cover-slips, bottle of water and of De Faure (all that is necessary) being packed in the microscope box or carried in the pocket. We now never use staining or balsam for mounting, as in it many fine chitinous structures are lost. Eggs and small larvae can be mounted direct in De Faure or Keilin without any previous washing or even killing. In

a day or two they are sufficiently clear for the internal structures to be seen. Or the larvae may be brought just to the boil, or merely warmed for a few minutes in 5 per cent. caustic potash solution, washed and mounted, when the internal chitinous structure will be much more clearly brought out. For the examination of Chalcid larvae and small Ichneumonids, it is best to prepare a few specimens by each method.

5. Microcryptus basizonius, Grav. **var. curtulus,** Kr.

M. basizonius is one of the commonest and most widely known parasites of *Diprion* species in Europe, although it has not been recorded from *Diprion polytomum*. Previous records of its European distribution and hosts are given below :—

Diprion frutetorum, F. ...	(Russia, Meier, 1927).
D. pallidum, Kl.	(Finland, Forsius, 1911).
D. pini, L.	(France, De Gaulle, 1919 ; Russia, Meier, 1927 ; Germany, Schutze and Roman, 1931 ; Poland, Sitowski, 1925–29 ; Holland, de Fluiter, 1932).
D. sertifer, Geoff. ...	(Russia, Meier, 1927 ; Poland, Sitowski, 1925).
D. similis, Htg.	(Finland, Forsius, 1911).
Banchus femoralis, Thoms.	(Germany, Habermehl, 1924, as hyper. ; also Scheidter, 1934).

So far only var. *curtulus* has been bred from *D. polytomum* cocoons in Europe, but *basizonius* has been found to attack *D. polytomum* very readily in the laboratory in England and in the field in Canada. As with all the cocoon parasites it is by no means easy to assess the true value of this parasite from the small samples of host cocoons it has been possible to collect. It is widely distributed in Czechoslovakia, from the lowest localities in mid-Bohemia to the heights of the Riesengebirge, and has been present in practically all the samples taken. It has never reached very high numbers, usually from 3 to 7 per cent., which figures certainly underestimate the total losses due to this parasite. Since, in biology and distribution, *basizonius* and var. *curtulus* have been found identical, it is perhaps permissible to consider the part played by the former as a controlling agent of the Pine Sawflies, which have been studied in large numbers, as an index of the value of this species. More especially from the practical point of view, since *M. basizonius* is the species imported into Canada in by far the greatest quantity, it is important to realise its possibilities. As a parasite of *D. sertifer* in the Riesengebirge Mountains it has been found parasitizing from 30 to 80 per cent. of the cocoons in different years. On the same host in Hungary its frequency varies from 10 to 52 per cent. in different localities and on different occasions. In the very extensive infestation in Sweden it accounted for 17·5 per cent. of overwintering cocoons in 1935, and 40 per cent. in 1936, by the end of which year the infestation had died down. On this host then, it forms a very considerable proportion of the parasite complex, which undoubtedly plays a major part in controlling this forest pest. On *D. pini* we have not the same amount of experience (27 million *D. sertifer* were collected in the past three years), but reliable records indicate the importance of *M. basizonius* on this host also. Recently, in Holland, de Fluiter (1932) records it parasitizing 36·5 per cent. of *D. pini* cocoons, and in Poland, Sitowski found it reaching 90 per cent. parasitism of the same host and considered that *M. basizonius* alone was responsible for reducing certain outbreaks of the Pine Sawfly.

The female of *M. basizonius* var. *curtulus* can be easily distinguished from the other parasites of *D. polytomum* by the following characters :—The pentagonal areolet of the forewing ; the reddish colour of the post petiole and segments 2, 3, and 4 of the abdomen, and the white speck on segment 7 ; and the white-banded antennae. The male is more slender than the female but has a similar pentagonal areolet and reddish abdomen, although the white area on segment 7 is much smaller. In the male the antennae are entirely black. Average length of male 6–7 mm. ; of female,

7–8 mm. Var. *curtulus* can be distinguished from *basizonius* by the absence of the white base to the hind tibiae, which is a marked character of the latter species ; by the abdominal segments, the first being weakly longitudinally striated, the second very weakly punctate, centrally basally the punctation closer and tending to be arranged in longitudinal striae. They both have filiform antennae, with the postannellus longer than the scape, thorax entirely black, and metathoracic spiracles small and subcircular.

This is a primary parasite of *D. polytomum*, ovipositing in the cocoon, in which takes place the whole of the larval development, the prepupa or pupa of the host being destroyed. Mating, which has been observed in the laboratory, takes place very soon after emergence. The male generally approaches the female from the front, strokes her antennae, then quickly mounts her and holds her in the mesopleural region with his front claws. The abdomen of the male is then flexed sideways and under the exserted ovipositor of the female to allow the insertion of the penis. After copulation, which usually occupies about half a minute, the female remains motionless for a short time and then proceeds to inspect the cocoons prior to oviposition. She first senses their shape by applying the surface of her antennae to them, then flexes the abdomen and bores with a slight circular motion through the hard integument. The sheath is now thrown free and the ovipositor works rapidly in and out of the aperture, as if stinging the host and testing its surface for egg-laying.

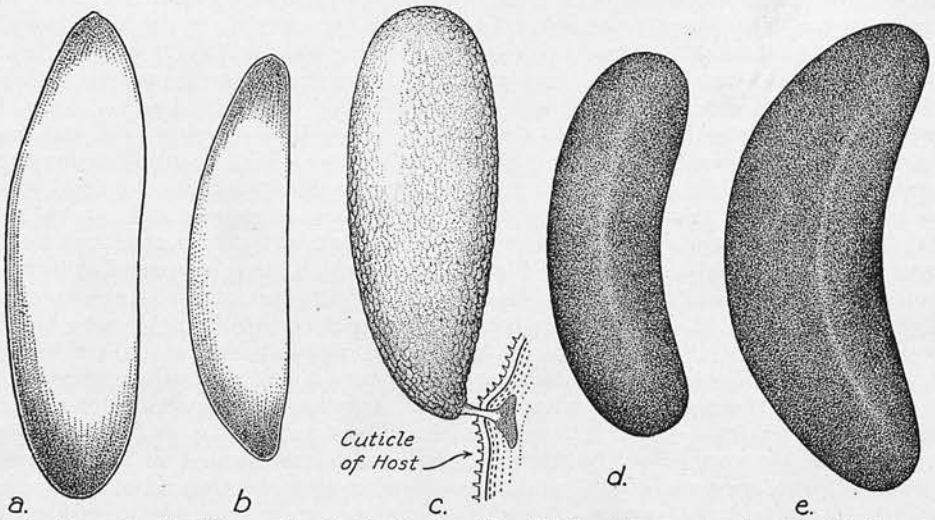

Fig. 1. Eggs of : (*a*) *Microcryptus basizonius* (× 45) ; (*b*) *Hemiteles areator* (× 45) ; (*c*) *Exenterus tricolor* (× 100) ; (*d*) *Holocremnus ratzeburgi* (× 75) ; (*e*) *Lamachus* sp. (× 75).

After a period of two or three minutes the ovipositor is slowly withdrawn and the egg is seen flowing down it. In one observation, during which the side of the cocoon was removed, the egg was seen emerging and swelling suddenly, the chorion hardening, leaving the egg lightly attached to the thoracic pleural region of the host. In many cases the egg was laid on the body in various positions without attachment. Females emerging from field collected cocoons at the normal time paralyse the host and render it inactive, but in laboratory-bred individuals this power of paralysing appears to get successively weaker and weaker, until ultimately very few of the prepupae are affected by the sting of the parasite. This will often result in the eggs being crushed by the active prepupa. Under laboratory conditions the parasite appears to be unable to distinguish between parasitized and unparasitized cocoons, since cocoons with two and three eggs were found in the rearing cages nearly as frequently as those with single eggs, although a fair supply of hosts was always present. From one cocoon

a maximum of twelve eggs was obtained, but this number occurred when two females were together in the same cage. As only one individual can arrive at maturity in one host, the laying of superfluous eggs in the same cocoon constitutes a distinct loss to the population. Under natural conditions, however, where the host material is more abundant and the range of the parasite so very much greater, this overlapping should be very infrequent. At laboratory temperatures (15–19°C.) the egg hatches in from three to four days after oviposition.

The egg (fig. 1*a*) is white in colour and opaque, somewhat sub-reniform in shape with one end tapering more acutely towards the micropyle, a tiny projecting knob. Conspicuous longitudinal striae are present on the chorion and its surface is dull, not shining. The average length of the egg is 1·3 mm. and average maximum breadth 0·35 mm.

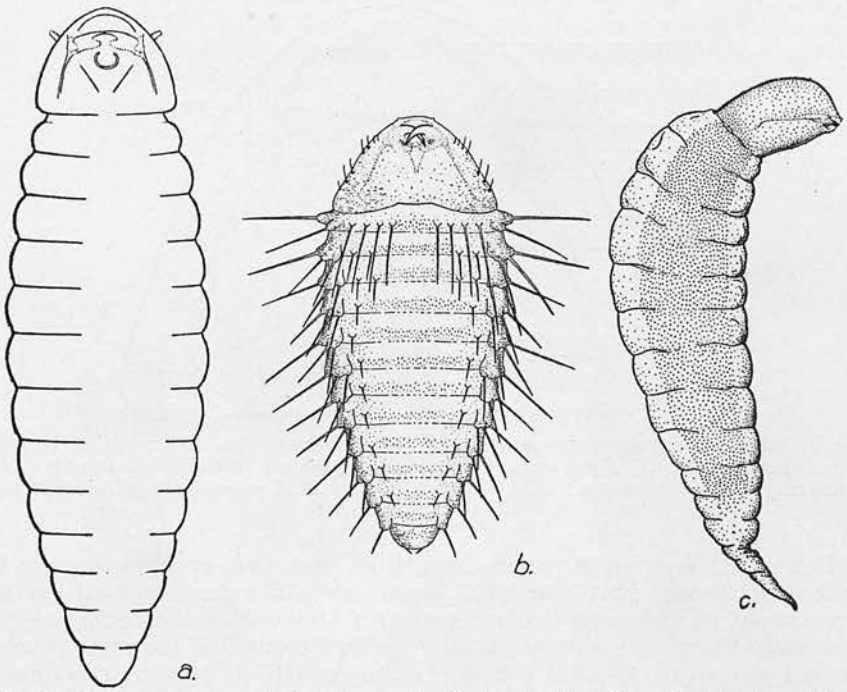

Fig. 2. Primary larvae of (*a*) *Microcryptus basizonius* (× 60); (*b*) *Exenterus tricolor* (× 100); (*c*) *Holocremnus ratzeburgi* (× 75).

On hatching, the primary larva is white in colour, the body surface being dull and the head glistening. It is fusiform in shape (fig. 2*a*) and consists of a head and 13 body segments, the apical segment being conical and slightly indented. The head is characterized chiefly by a pair of conspicuous antennae, a pair of curved mandibles and a fairly well chitinized internal skeleton, while the skin of the body is covered with small triangular-shaped spinules. The mouth-parts and supporting skeleton (fig. 3) are similar in outline to those of the mature larva, except that the mandibles are curved (straight in four succeeding instars) and less strongly chitinized, the labial struts are absent and do not appear until the second stadium, and the labial and maxillary sensory papillae are represented only by tiny dots. In length the newly-hatched larva measures 1·44 mm. by 0·36 mm. in breadth at the middle. When actively feeding, the larva throughout its five stages is dark greyish-green in colour, except for the head, first three and tenth segments, which are whitish. At the end of the feeding stage this green colour gives place to a dark creamy-white.

The larvae of *Microcryptus* during development pass through five stadia. At room temperatures (15–19°C.) and humidity (50 per cent. R.H.) the length of time passed in the first stage is two to three days; in the second, two to three days; in the third, three days; in the fourth, three days; and in the fifth, up to the end of feeding, three days. When the mature larva has finished feeding it begins to spin its cocoon (this marks the beginning of the prepupal stage), which it completes in from three to four days. A further twelve to thirteen days are spent within the cocoon in the prepupal and pupal stages, and the fully-formed adult emerges 33 days after the egg has been laid. In the constant temperature and humidity room, where the temperature is much higher (22°C. and 70 per cent. R.H.) these times are shortened and the entire life-cycle is completed in 24 days.

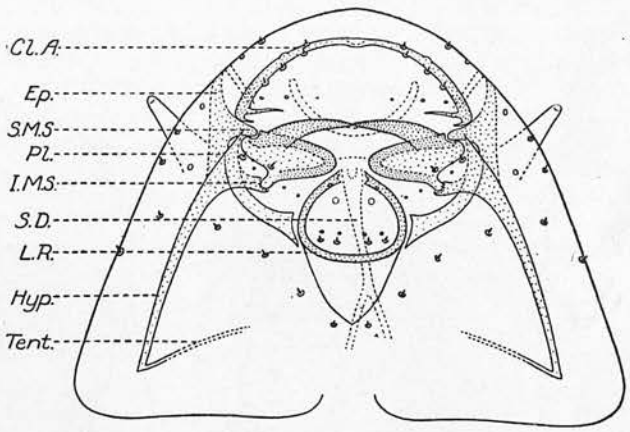

Fig. 3. Head of primary larva of *Microcryptus basizonius* (× 150): *Cl.A*, clypeal arch; *Ep*, epistoma; *Hyp*, hypostoma; *I.M.S*, inferior mandibular strut; *L.R*, labial ring; *Pl*, pleurostoma; *S.D*, salivary duct; *S.M.S*, superior mandibular strut; *Tent*, tentorium.

In Bohemia *Microcryptus* passes through at least two, or more usually three, generations in the year in cocoons of *D. polytomum*. The parasites that overwinter as prepupae pupate and emerge early in spring, in April or May, before the sawfly host emerges, and immediately oviposit in unparasitized cocoons of the same generation. The second generation of adult parasites emerges early in July, at the time when cocoons of the first generation of *D. polytomum* are formed, and immediately commences oviposition. The third generation of parasites emerges in September and oviposits on the second generation cocoons of the host, in which hibernation of the parasite prepupae takes place. On *D. sertifer* in Bohemia there are also three generations, but on the same host in Hungary, four generations may be passed in the year. Here the spring is earlier, autumn is mild and late, and the summer temperature high, so that there is a longer active period and the parasite's life-cycle is shortened. Also, in the case of this host, cocoons are available through the whole summer.

The mature larva (fig. 4*a*), which measures 9 mm. in length by 4 mm. in breadth at the middle, is somewhat cylindrical in shape with both ends tapering narrowly. The ventral side is flattened and the dorsal strongly convex. It consists of a head with strongly chitinized mouth-parts and supporting skeleton and 13 body segments. Dorsally, in segments 4 to 10, there are conspicuous curved transverse swellings, while in segments 4 to 11 hypopleural lobes are present. Ventrally on each of the first three segments, a pair of small papillae (vestigial legs) can be distinguished. The cuticle of the body, which is slightly shiny, is covered with small spinules,

while the cuticle of the head is very shiny and glabrous. Under the high power of the microscope the skin armature (fig. 16*a*) can be seen to consist of fairly regular rows of small, bluntly pointed, conical scales or spinules, with wide, rounded bases. They measure 0·01 mm. in height and are approximately the same width at the base, being purely cuticular structures. There are also occasional sharp, strong microsetae, 0·02 mm. long, scattered over the body segments. These are articulate, trichoid, and probably hypodermal in origin. The tracheal system is of the usual Ichneumonid type, with accessory thoracic branches to the longitudinal trunks and nine pairs of spiracles. The spiracles (fig. 15*a*) are fairly large and well chitinized, and consist of three distinct parts, an atrium, a short connecting stalk, and a closing apparatus. The atrium is very broadly pear-shaped, the flattened, broader end bearing the very small external opening, the lower, narrower end joining the stalk. It has rather irregular annular thickenings to the sides, and is 0·035 mm. broad. The short, annulated stalk is 0·018 mm. wide, and leads into the closing apparatus with much thickened walls and a narrow central meatus. This leads into the trachea. The whole spiracle is 0·075 mm. long.

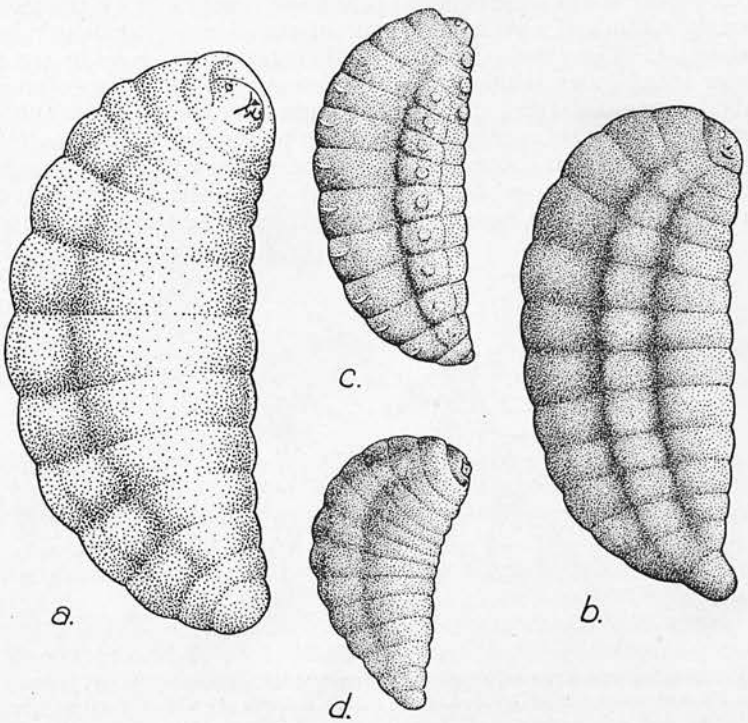

Fig. 4. Mature larvae of (*a*) *Microcryptus basizonius* (× 10); (*b*) *Holocremnus ratzeburgi* (× 9); (*c*) *Exenterus tricolor* (× 7); (*d*) *Hemiteles areator* (× 6).

The chief features of the head are the strongly chitinized mouth-parts and supporting skeleton, which stand out very clearly through the cuticle; the dorso-anterior epicranial lobes, which are clearly demarked by the metopic suture; the temporal fossae, which are darkened vertical areas, one on each side of the epicranial lobe just above the antennae; the antennae, which are small but have large conspicuous concentrically ringed bases; and the triangular area above the clypeus, clearly marked off by the frontal sutures. The mouth-parts consist of clypeus, labrum, mandibles, maxillae, labium, salivary duct, ligula, and maxillary and

labial palps or sensory processes. On the upper margin of the colourless clypeus there is a strongly chitinized transverse arch, the clypeal arch. This arch is not present in all Ichneumonid larvae, but appears to be a fairly constant feature of the Cryptines, in many cases affording a useful distinctive character. On each side of the clypeus, close to the clypeal arch, there are three setae and a pair of sensillae. Two further pairs of sensillae are present on the thin and colourless labrum. The mandibles, which are strongly developed on a sub-quadrate base, are provided with two rows of fairly strong bristles. Two slight unchitinized swellings beneath the mandibles constitute the maxillae. Each bears a maxillary palp and three pairs of setae. The maxillary palp is made up of a pair of sensory pits, the inner circular and the outer semi-circular, both of which are enclosed and surrounded by a lightly pigmented chitinous ring, the whole process being slightly raised. This structure gives the palpi a figure 8 appearance under low magnification. The cuticle of the maxilla is attached laterally to a thin inward projection of the maxillary strut. Between and below the maxillae is the colourless labial area, marked out by the labial ring. It bears a pair of processes similar to those on the maxillae—the labial palps. Below these are two pairs of strong setae. The opening of the salivary duct is situated between the two upper ends of the labial ring just below the mouth opening. It is strongly chitinized and bears a pair of sensillae. Underneath is the lightly chitinized ligula. The chief structures of the supporting skeleton are the superior and inferior mandibular struts, the pleurostoma, epistoma, hypostoma, maxillary struts, labial struts, labial ring, clypeal arch, and tentorium. The mandibles articulate on the superior and inferior mandibular struts by means of a ball and socket joint. In the lower articulation a condyle on the mandible articulates in a fossa on the inferior mandibular strut, while in the upper this order is reversed, the condyle being on the strut and the fossa on the mandible. The two mandibular struts are

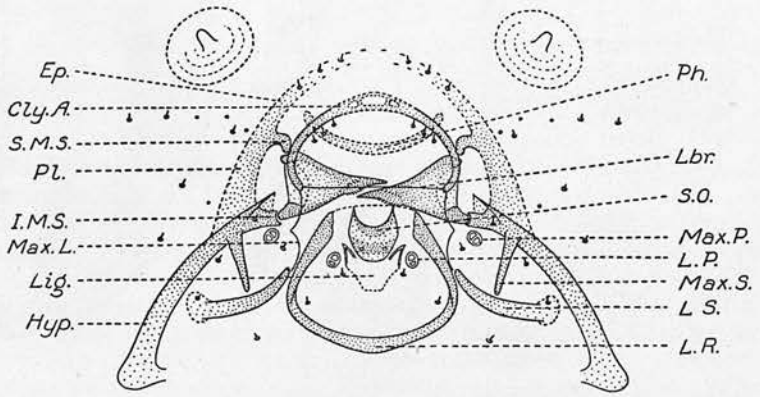

Fig. 5. Mouth-parts of mature larva of *Microcryptus basizonius* (× 60); *Cly.A*, clypeal arch; *Ep*, epistoma; *Hyp*, hypostoma; *I.M.S*, inferior mandibular strut; *Lbr*, labrum; *Lig*, ligula; *L.P*, labial palp; *L.R*, labial ring; *L.S*, labial strut; *Max.L*, maxillary lobe; *Max.P*, maxillary palp; *Max.S*, maxillary strut; *Ph*, floor of pharynx; *Pl*, pleurostoma; *S.M.S*, superior mandibular strut; *S.O*, salivary opening.

joined together on each side by the pleurostoma, which continues above the clypeus as the epistoma. This latter forms a discontinuous arch to which the thin anterior arms of the tentorium are attached. On its surface the epistoma bears three pairs of setae. The inferior mandibular strut is continued latero-ventrally, as the hypostoma, to join up with the internal posterior arms of the tentorium. About one-quarter along its length, the hypostoma sends off the maxillary strut into the maxilla. The labial area is defined by the incomplete U-shaped labial strut. The only other chitinized structure present in an external view of the face is the darkened floor of

the pharynx which, on focussing down under the microscope, appears as an inverted arch. In addition to the setae, already mentioned, there are two further groups outside the main skeletal system, a group of three on each side of the lower part of the pleurostoma, and one of six higher up in this area and external to the superior mandibular struts.

The liberation of this valuable parasite in Canada was advised from the very first. In 1933, 397 individuals of *M. basizonius* were liberated, a large number of which had been bred throughout the winter in the laboratory at Farnham Royal, most of the remainder coming from a *D. sertifer* infestation in the Riesengebirge. In 1934, 63,000 individuals were liberated, having been collected from big infestations of *D. sertifer* in the Riesengebirge and in Hungary. In 1935, 64,000 were liberated, the majority from the same host from Sweden and Hungary, but a small proportion of these, probably not more than 2,000, being the var. *curtulus* from *D. polytomum* in Bohemia. In 1936, 3,483 specimens were liberated, half of which were var. *curtulus* from *D. polytomum*, the remainder from *D. sertifer* from Sweden and Hungary. Thus a total of 131,205 parasites has now been liberated. The true *M. basizonius* had established itself in the Canadian infestations by 1935, when it was recovered from *D. polytomum* cocoons there. With this encouraging start there is every reason to hope that *M. basizonius* may eventually prove as effective a check on *D. polytomum* in Canada as it is on the other *Diprion* species in Europe. In considering the chances of its success, one important point must be remembered. In Canada quite a large proportion of the sawfly prepupae go into diapause every year, remaining in the cocoons for 2, 3, or even 4 years. This ensures a constant and plentiful supply of hosts, and, as has been pointed out, this cocoon parasite can develop three or even four generations in the year to the host's two. This results in a quicker reproductive rate on the part of the parasite, making the chances of its overtaking the host and eventually controlling it very much greater.

6. Leptocryptus aereus, Grav.

Previous records of this species show that it has often been bred from Lepidoptera, in many cases being definitely quoted as secondary. During the investigations it has turned up occasionally in batches of *D. polytomum* cocoons from different regions in Bohemia, though never in numbers. It occurred in greatest abundance at Kout in the Böhmerwald in 1934, when 8 per cent. of the cocoons produced this species. At the same time the total parasitism was high—67 per cent. Since then it has never appeared in more than 1 or 2 per cent., mainly from the Böhmerwald and South Bohemia.

This small, neat species is fairly easy to recognise by its size alone, never exceeding 5 mm. in length, usually much less, with slender, long-petiolate abdomen, large wings, and long, curved antennae. Head and thorax black and abdomen almost entirely red, except for the petiole, which is black with a red spot centrally posteriorly, and segments 2 and 3, which are black antero-laterally. Metathorax heavily punctate, with areolation present, but weakly developed. Areole pentagonal with outer side missing. Ovipositor short, 0·8 mm., or approximately one-third the length of the abdomen.

L. aereus is hyperparasitic upon various parasites of *D. polytomum*. It has been found destroying the larvae of *Exenterus*, *Holocremnus*, and *Lamachus*, and may attack others. It is possible that it will act as a primary upon the sawfly, but this has not yet been found in examining cocoon remains, and laboratory experiments have failed to demonstrate this. Two or three eggs are usually laid through the cocoon when the primary parasite is fairly well developed. In more than half the cases observed two parasites have succeeded in reaching maturity and emerging.

It is hardly necessary to point out the danger of such a confirmed hyperparasite in Canada.

7. Spilocryptus abbreviator, F.

This parasite has been bred from a few Lepidopterous hosts in Great Britain. We have no records from the Continent, and none from Hymenoptera. During the present work it was obtained very occasionally from the cocoons of *D. polytomum* from the lower-lying localities in Bohemia, especially in the Brdy Wald Region. In 1936 it was present in 3 per cent. of cocoons from that region, and in 5 per cent. of cocoons from Hradec in Silesia, from which locality the variety *hopei*, Grav., was obtained at the same time.

This is the only parasite of *D. polytomum* with short, rudimentary wings, otherwise it resembles very closely *Microcryptus*, and there is no danger of confusing it with the various species of *Gelis*, which have no wings at all. The following characters are sufficient to recognise it among the Cryptines : Head and thorax black, occasionally scutellum red. Abdomen reddish yellow, with the last three segments black above, the last segment tipped with white. Antennae three-coloured ; basal portion (nearly half) reddish, middle four segments white, distal portion dark brown. The rudimentary wings just reach to the end of the metathorax but not as far as the petiole. The posterior femora are distally brown, posterior tibiae apically dirty white. Only females are known. Specimens from *D. polytomum* varied from 3·5 to 6·0 mm. in length, with the ovipositor two-thirds the length of the abdomen.

This species has been found attacking *D. polytomum* always as a primary parasite, laying its egg in the cocoon, the larva feeding externally on the prepupa, which is rarely completely eaten because of the rather small size of this parasite.

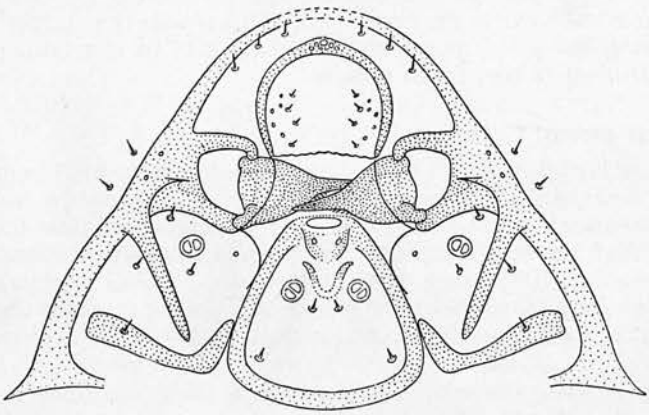

Fig. 6. Mouth-parts of mature larva of *Spilocryptus abbreviator* (× 107).

In its larval stages this parasite is fairly easily distinguishable from the other parasites, although the head skeleton and skin armature resemble closely those of the other Cryptines. The head skeleton (fig. 6), however, has one very marked feature distinguishing this species, that is the horseshoe-shaped clypeal arch, very distinct from the broad, flattened structure of the others. Again, the epistoma is almost complete, much more so than in *Hemiteles* or *Microcryptus*. The labial struts are distinctly angled where they join the labial ring. The region round the salivary opening is distinctly, though not heavily, chitinized. The ligula is distinctly visible as a small, wide-spreading U. The skin of *Spilocryptus* (fig. 16*b*) is covered with regular rows of sharply conical spinules, from 0·015 to 0·12 mm. in height. These are much more sharply pointed and of narrower base than the strong, blunt spinules of *Microcryptus*, and stronger and longer than those of *Habrocryptus*. There are also sparsely scattered microsetae, 0·04 mm. in length. The spiracle (fig. 15*b*), 0·07 mm. long, is large and stumpy, the atrium globular, with a reticulate strengthening of the

walls somewhat similar to the spiracle of *Exenterus*, quite unlike the other Cryptines. A short, broad, annulated stalk leads to the well developed, thick-walled closing apparatus.

In the few instances when this insect has been recovered from *D. polytomum* cocoons, it has always been a primary parasite and there is no reason to suppose of its being otherwise. In view of the Cryptine's ability to go through several generations to the host's two in Europe, it certainly seems worth introducing this, as well as the other Cryptines, into Canada, where the ever-present supply of cocoons makes this habit especially valuable. The insect seems to prefer a low locality, below 500 m., with warm, sunny climate and not heavy rainfall.

8. Habrocryptus polytomi, Tschek.

The only previous record we can find of this insect is in Tschek's original description (Tschek, 1872), when it was bred from *D. polytomum* in Austria. It has occasionally turned up in Bohemia, bred from cocoons collected from spruce branches, but has never been abundant, at the most in 2 per cent. of the cocoons. It has always appeared in the lower and warmer localities, such as Dobřiš, the Sazava River region, and the lower parts of South Bohemia, Neu Bistritz, and Pleše.

The adult insect is easy to recognise, having the typically Cryptine features of a fine, right-angled petiole and large pentagonal areolet, together with a plain black head, thorax, and abdomen. It is most easily confused with *Hemiteles sordipes*, from which it may be distinguished by the absence of metathoracic areolation, by the white spot on the middle segments of the black antennae, and the areole being closed or, at most, with the outer side very faint or missing on one side, never entirely open on both sides. The black body is slightly polished, having very fine punctation. The second abdominal segment is edged with pale brown. The antennae are black, with the middle two or three segments white above only, not with a complete white ring. Legs dark reddish-brown, hind tibiae almost black. The metathoracic areolation is entirely wanting. Spiracles small and round. Length, 5 mm. Ovipositor half the length of the abdomen, or 1·5 mm.

In all the cases observed this has been a primary parasite of *D. polytomum*, laying its eggs in the cocoon and the larvae feeding externally on the sawfly prepupae or, occasionally, pupae.

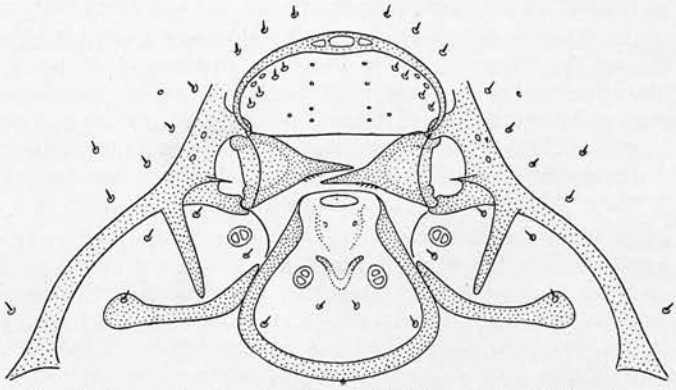

Fig. 7. Mouth-parts of mature larva of *Habrocryptus polytomi* (× 107).

The larva is very similar to those of the other Cryptines and can only be separated on microscopic distinctions. The general outlay of the larval head skeleton (fig. 7) is essentially similar to that of *Microcryptus* or *Hemiteles*. From both it can be

distinguished by the very weakly developed epistoma and the arrangement of setae and sensillae on the labrum. It differs from *Microcryptus* in not having the strongly chitinized salivary opening and in the smaller and differently shaped ligula ; from *Hemiteles* in the smaller, more chitinized ligula, V-shaped rather than Y-shaped, and in the structure of the clypeal arch. The chitinized floor of the pharynx can be seen in preparations, but is not included in the drawing for the sake of simplicity. The skin structure (fig. 16*c*) is quite distinct from that of either of the above species, resembling very closely *Spilocryptus*, but with shorter, weaker spinules, never more than 0·015 mm. long and more likely to be bent and twisted. There are occasional microsetae, 0·025 mm. long. The spiracle (fig. 15*c*) is quite distinctive, rather short, less than 0·07 mm. long over all, with the atrium shaped like a Chinese ginger jar, with a number of fine, annular thickenings, the stalk coarsely annulated, having the appearance of four globes end to end, and a small closing apparatus.

This is one of the least important parasites of *D. polytomum* in Europe, but, as it is undoubtedly a primary and probably monophagous, it would be worth making some experimental liberations in Canada in the heavily infested areas. From its distribution in Europe, a lowish altitude, not above 500 m., with a warm climate, would be most suitable.

9. Hemiteles areator, Panz.

This species has been recorded from at least twenty-eight different hosts, some of which are *Apanteles glomeratus, A. solitarius, Microcryptus basizonius, Meteorus versicolor, M. pulchricornis, M. ictericus, Diprion pini, Hemerobius stigma, Chrysopa nigricornis, Hyponomeuta padella*, etc. It has a wide distribution and is one of the commonest species of *Hemiteles*. In the course of the present investigations, this parasite has appeared regularly in samples of cocoons of *D. polytomum* collected from all over Bohemia. Although usually present in small numbers, only 1 to 5 per cent. of cocoons, it can occasionally attain a fairly high degree of parasitism ; for example, 15 per cent. at Neu Bistritz in South Bohemia in 1934, and 10 per cent. in the Böhmerwald region in the same year. It has always been most abundant in the South Bohemian and Böhmerwald mountains, of regular occurrence but in small numbers in the low-lying, warm middle Bohemian areas, and absent from Silesia. It was bred from *D. sertifer* cocoons from the Riesengebirge Mountains in 1933 and 1934, where it was mainly hyperparasitic. Another species, *H. inimicus*, was far more prevalent as a hyperparasite on this host in the same locality.

This is the only Ichneumonid parasite of *D. polytomum* with dark markings on the wings. Among the HEMITELINI it may be distinguished by the following characters : Coloration rather variable, with head, thorax and abdomen black with a variable amount of brown-red markings ; legs mainly red ; ovipositor rather less than half the length of the abdomen ; thorax with strong punctation, metathoracic areolation fully developed ; wings with three dark bands ; areolet regular, pentagonal, but with outer side missing. Length from 2·5 to 5·0 mm.

As can be seen from the host records, *H. areator* is frequently hyperparasitic. As is often the case with a Hymenopterous host, it can act either as a primary or secondary parasite on *D. polytomum*. In rather less than half the cases observed it has been primary on this host ; in the majority of cases it has been hyperparasitic upon *Exenterus, Holocremnus, Lamachus* and *Microcryptus*. Eggs (fig. 1*b*) are laid in the host cocoon ; the larvae feed externally on host or parasite.

The mouth-parts and supporting skeleton of the mature larva (fig. 8) are very similar to those of *Microcryptus basizonius*, but the two can be separated by the following distinctions : (1) By size, the area of the mouth-parts and skeleton in *Hemiteles* being only two-thirds as large as that of *Microcryptus* ; (2) by the shape of the ligula ; in *Hemiteles* this is shaped like a wide tuning-fork, in *Microcryptus* it

consists mainly of two small triangular pieces underneath the chitinization of the salivary duct; (3) by the chitinization of the salivary duct below its opening, this area being more weakly chitinized in *Hemiteles* than in *Microcryptus*; (4) by the mandibles, those of *Hemiteles* being much more finely pointed than those of *Microcryptus*; also the bristles on the mandibles of *Hemiteles* are small, whereas in *Microcryptus* they are large and conspicuous; (5) by the zenith of the clypeal arch; in *Hemiteles* this is broader and has greater areation than in *Microcryptus*. It is most likely to be confused with *Habrocryptus polytomi*, which it closely resembles in size and head skeleton. Points which distinguish it are the more complete epistoma of *Hemiteles*, the different structure of the clypeal arch, the Y-shaped, weakly chitinized ligula, and the arrangement of the sensillae on the labrum. The skin structure of *H. areator* (fig. 16*d*) is quite distinctive, consisting of a number of small, closely arranged papillae, at most 0·005 mm. high, with rounded, dome-shaped ends. These are quite unlike the sharp-pointed spinules of *Spilocryptus* or *Habrocryptus*, or the stronger, blunter ones of *Microcryptus*. There are sparsely scattered

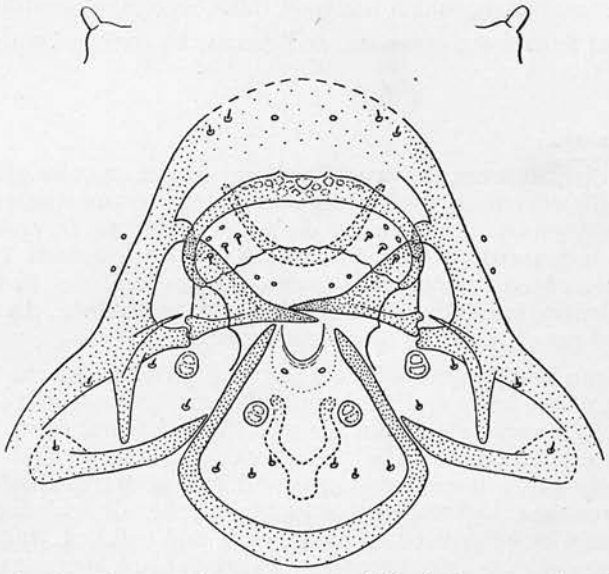

Fig. 8. Mouth-parts of mature larva of *Hemiteles areator* (× 107).

microsetae, 0·025 mm. long. The spiracles (fig. 15*d*) further serve to distinguish this from the other Cryptines. A regular, bluntly pear-shaped atrium has three annular thickenings, and surmounts a long, annular stalk, 0·045 mm. long, below which is a rather long, narrow closing apparatus. The whole spiracle is of a long and slender type, with an over-all length of 0·1 mm.

This species is so frequently hyperparasitic on the most important larval parasites of *D. polytomum* that its liberation in Canada, at the present state of our knowledge, is considered very inadvisable.

10. Hemiteles sordipes, Grav.

The only records of this species are as a hyperparasite and it has been recovered from *D. polytomum* cocoons on one or two occasions from the Brdy Wald area in mid-Bohemia, in every case as a secondary on the larval parasites *Exenterus* and *Lamachus*.

This species may be distinguished among the parasites of *D. polytomum* by the Hemiteline characters of the large, pentagonal areolet with the outer side wanting,

and the complete areolation of the metathorax, together with its uniform, black coloration of the head, thorax and abdomen, only the legs being reddish. Further distinctions among the Hemitelines are afforded by the long, thinnish antennae; the ovipositor as long as the abdomen; the very good development of the lines dividing up the areolation on the metathorax; and the hyaline wings. Length, 4 mm.

It is unnecessary to describe the life-history or larvae of this hyperparasite, and needless to say, it should be withheld from liberation in Canada.

11. Gelis acarorum, L. (Pezomachus acarorum, L.) and Gelis sp.

There are only two previously recorded hosts of *G. acarorum*, in each case as a secondary, from *Microgaster tibialis*, Nees, and *Apanteles gracilipes*, Thoms. The majority of the members of this genus seem to be hyperparasitic. One or other of the species of *Gelis* are bred occasionally from *D. polytomum* cocoons collected in the field. It is never numerous, which is a good thing, as it is invariably hyperparasitic.

Both male and female are apterous, and cannot be confused with other parasites of *D. polytomum*.

12. Delomerista sp.

This genus, distinct from the true Pimplines (see characters given below), is at present in such disorder that it is impossible to assign to any species those examples bred from *D. polytomum*. It certainly does not belong to *D. pfankuchi*, Brauns, the only species undoubtedly recorded from pine sawflies (Sitowski, 1925; de Fluiter, 1932). It has been bred from cocoons from only two localities, in the Böhmerwald and in South Bohemia, in 1934, and has not been seen again since. In the Böhmerwald it was found in 4 per cent. of the cocoons examined.

This species can be distinguished from the other parasites by the sessile abdomen, black coloration of the body and the long ovipositor (at least half the length of the abdomen). It can be separated from the true Pimplines and other *Delomerista* spp. on the following characters: The metathorax has the central areolation very distinctly developed, the area superomedia and area posteromedia being completely enclosed. The area basalis is hardly recognisable and the side fields are not marked off. Head and antennae entirely black. Thorax black and polished, with puncturing and hairing, except on metathorax, very weak. Abdomen black, more strongly punctured, giving a less shiny appearance. The fourth, fifth, sixth and seventh, and sometimes third, abdominal segments have dull, dirty-yellow hind margins. The first two pairs of legs are entirely reddish yellow; hind legs of the same colour, except the tibiae (brown, white basally), and tarsi brown. Length from 6 to 8 mm. Ovipositor from 2 to 2·5 mm. long.

This is a primary parasite of *D. polytomum*, laying its eggs through the cocoon on the prepupa or pupa, upon which the larvae feed externally. The mature larva does not spin any cocoon, but remains through the prepupal and pupal periods naked in the host cocoon. This affords one means of separating *Delomerista* and *Pimpla* larvae and pupae from those of all the other Ichneumonid parasites. Further than this the larval skin structure and mouth-parts make the immature stages of *Delomerista* quite unmistakable.

The structure of the mouth-parts and supporting skeleton (fig. 9) exhibit only certain of the true Pimpline characters, together with some features typical of the CRYPTINAE. This is especially interesting in view of the way these two groups merge one with another in adult morphology. The Pimpline characters lie in the labial ring, very much thickened basally, the much reduced labial struts, and the shape of the mandibles, with long, strong teeth, bristly on the interior aspect only, and with

broadly rounded bases. It differs from *P. alternans* in the full development of the hypostoma, the incomplete or weakly developed epistoma, the presence of a well developed clypeal arch and the absence of a spiny armature at the base of the pharyngeal opening. The presence of a clypeal arch is a typical Cryptine character, as is also the incomplete epistoma. The skin structure of *Delomerista* (fig. 16*e*) affords an easy means of identifying the larvae. In the first place it is the only larva, apart from *Monodontomerus* among the Chalcids, that is hairy. The hairs (macrosetae) are neither very close nor very long (0·1 mm. in length) compared with those of *Monodontomerus*, yet they are sufficient to give the larvae a hairy appearance without the aid of a microscope. Microscopically the skin is covered with quite large (0·01 mm. diam.) dome-shaped papillae, regularly spaced and not very close together. The spiracle (fig. 15*f*) is small and very simple, consisting of a perfectly plain, round atrium, 0·02 mm. in diameter, a straight narrow, annulated stalk, and normal type of closing apparatus above the trachea. The combination of these characters makes this a very easy larva to recognise.

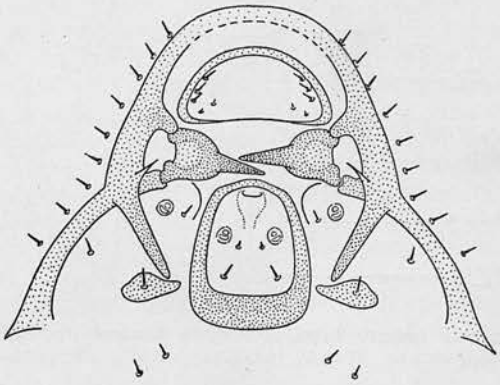

Fig. 9. Mouth-parts of mature larva of *Delomerista* sp. (× 107).

In view of the primary nature of this parasite and the fact that it can attain appreciable parasitism on *D. polytomum* in Europe, despite its rare appearance, it is certainly worth making experimental liberations of this species in Canada on the chance that it may find a set of conditions more suitable for increase. Judging by its limited appearance in Bohemia, it is partial to wooded, hilly country of not too great an altitude, between 400 and 600 metres, and with a moderate annual rainfall of about 500 mm.

13. **Pimpla (Itoplectis) alternans,** Grav.

This decidedly polyphagous parasite has been recorded from a variety of insect hosts, mainly Lepidoptera. There are two records from pine sawflies, both from *D. pini*, in France (de Gaulle, 1919) and Germany (Scheidter, 1934). During the present work this species and a variety, *kolthoffi*, Aur., were found fairly frequently parasitising *D. sertifer* in the Riesengebirge in 1933 and 1934. It has only occurred on *D. polytomum* in one locality and in one season, at Hradec in Silesia in 1936, when it was present in approximately 2 per cent. of cocoons collected from the ground. As with most other parasites of the cocoon stage, this paucity of records is misleading, in view of the small number of cocoons collected in previous years. Only in 1935 and 1936 were large numbers of cocoons collected which had had a reasonable exposure to natural attack by parasites. Many of the rarer parasites were found in these years.

This species may be distinguished from the other parasites of *D. polytomum* by the sessile abdomen, uniformly black coloration of head, thorax and abdomen, the absence of metathoracic areolation and the long ovipositor, approximately one-third of the length of the abdomen. It may be distinguished from the other Pimplines (being set aside by Thomson in a separate genus, *Itoplectis*) by the following characters : The groove before the mesepimeron is not angled opposite the punctiform fovea ; the last joint of the hind tarsi is distally longer than the second ; the thorax is polished and with only a very light covering of hairs, which by no means obscure the colour ; the fore legs are a bright reddish-yellow to yellow ; the hind tibiae three-coloured, with three dark brown rings, a broad one at base, a narrower one before the middle and one at the apex, white between the basal and middle ring, red between the middle and apical. Length, 7 mm. Ovipositor, 1·5 mm.

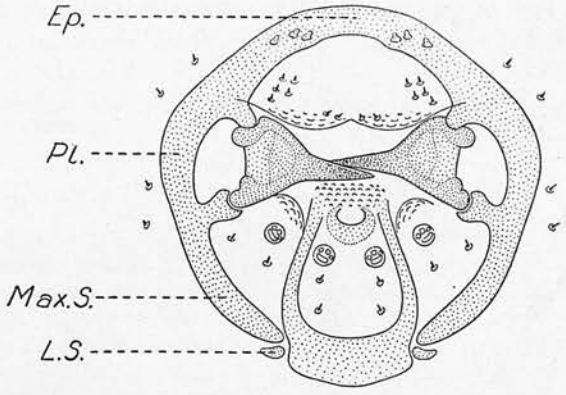

Fig. 10. Mouth-parts of mature larva of *Pimpla alternans* (× 107) : *Ep*, epistoma ; *L.S*, labial strut ; *Max.S*, maxillary strut ; *Pl*, pleurostoma.

In the cases that have come under our own observation, in both *D. sertifer* and *D. polytomum*, this is a primary parasite. It oviposits on prepupae or pupae within the host cocoon and the larva feeds externally. On the completion of feeding the mature larva does not spin any sort of cocoon, but enters the resting period naked in the host cocoon. In this way the mature larvae and pupae of this insect and of *Delomerista* can be distinguished from those of all the other Ichneumonine parasites of *D. polytomum*, which invariably spin a thin, papery cocoon within the host cocoon, in which the prepupae and pupae rest.

The larval mouth-parts (fig. 10) are very characteristic and at once set this aside from all the other parasites. The hypostoma is entirely wanting, and the epistoma, pleurostoma, and maxillary struts form an almost complete ring, broken at the bottom to admit the labial ring. This is of characteristic Pimpline form, strong, and with broad, thickened and rather flattened basal segment. The labial struts are reduced to mere vestiges, this being another Pimpline characteristic. The mandibles are strong and coarse, the inner aspect of the heavy, pointed teeth being armed with bristles. The labrum and maxillary lobes are covered with small, round projections giving them a warty appearance. The labium is armed with a close array of small, sharp, triangular teeth. The labial and maxillary palps have not the appearance common to those of the other Ichneumonines. Instead of two large pits surrounded by a pigmented ring, giving a figure 8 appearance, there are three or four small pits on the inner aspect (nearest the mouth) and one large curved pit outside these. The whole group is surrounded by a pigmented chitinous ring. In general, the head-capsule of the *P. alternans* larva is strong and well chitinized, and the mouth-parts very strongly chitinized, making them stand

out conspicuously. The skin armature (fig. 16*f*) is peculiar to this species, consisting of small conical scales, equilaterally triangular in longitudinal section, not very thickly but regularly distributed. Besides these there are occasional small setae, never more than 0·03 mm. in length. The spiracles (fig. 15*e*) are absolutely characteristic, distinctly larger than in any other of the larvae, with a short, very broad stalk joining direct on to the trachea, without the intervention of a closing apparatus as in the other spiracles described. The atrium is a large, rather flattened sphere 0·045 mm. in diameter, with a very small external opening, less than 0·015 mm. in diameter. The inner wall of the atrium is lined with a number of short projecting processes all radiating towards the centre of the sphere. The stalk of the spiracle is formed of one ring and a large pear-shaped vessel, the lower end of which is divided by sutures into 6 petal-like components, which closely adhere together, clasping the end of the trachea.

This species has been found only as a primary parasite on the DIPRIONIDAE but there seem to be cases in which it acts as a hyperparasite among Lepidopterous hosts. This, however, should not be sufficient to condemn it as a sawfly parasite, and there are several good practical arguments for its introduction into Canada. In the first place, its extremely polyphagous habits make it peculiarly suitable for the two extreme ends of an infestation. In localities newly invaded by the sawfly, where it is not yet in sufficient numbers to maintain monophagous parasites, the more polyphagous species, such as *Pimpla alternans*, might be able to maintain themselves on a variety of hosts. As the sawfly increases in numbers, it would come in for more and more attention as a host. Thus, this is a particularly suitable species for use as a barrier against the spread of *D. polytomum*. Similarly, it would be able to maintain itself in cases of severely reduced populations of the sawfly, where the numbers of primary parasites would fall to negligible proportions. Another practical advantage possessed by this Pimpline is the possibility of obtaining it in really large numbers from one or other of its alternative hosts.

14. **Mesochorus thoracicus,** Grav., **M. fulgurans** Curt., **aud M. (?) dimidiatus,** Holmgr.

A great diversity of insect families is attacked both by *M. thoracicus* and *M. fulgurans*, which are two of the commonest members of the genus, with a wide distribution in Northern and Central Europe. *M. dimidiatus* is uncommon. The main host records for *M. thoracicus* are *Peronea maceana, Microgaster* sp., *Tachina* sp., *Tortrix viridana, Agelastica alni, Chrysomela varians,* and *Galleruca lineola*; for *M. fulgurans—Diprion pini, D. laricis, D. variegatus, Ceromasia inclusa, Trophocampa* sp., on *Abraxas grossulariata,* and *Eupithecia pimpinellaria.* The genus is thought by Sitowski (1925–29) to be entirely hyperparasitic and this is probably the case with *M. thoracicus* and *M. fulgurans*, so far as the records indicate, although an examination of the cocoon from which *M. thoracicus* emerged showed a trace of the larval skin of a primary parasite. Only one individual of each species was bred out. They emerged from first generation cocoons of *polytomum* collected as larvae in Tyssa, North Bohemia. Because of their rarity and comparatively unimportant status as probable hyperparasites, no data have been obtained on their biology.

The MESOCHORIDES can be recognised among the other Ophionine tribes by the conspicuously large rhomboidal areolet, strongly shining body, and the pair of elongate styloid appendages in the male. These characters will also separate them from the other parasites of *Diprion polytomum*, while the following colour table will separate them from each other.

	M. fulgurans	*M. thoracicus*	*M. dimidiatus*
Head	Light reddish-brown	Female black; male reddish-brown	Reddish-brown
Thorax	Reddish-brown	Reddish-brown, mesonotum flecked with black at middle, metanotum black	Black
Abdomen ...	Reddish-brown	Black, hinder edges white	Female, segment 1–2 or 3 black, with light edges, 4–7 reddish-brown; male black, segments 1 and 2 with light hind edge, 3 reddish-brown

Because of their hyperparasitic habits care should be taken not to liberate any of these species in Canada.

15. Holocremnus ratzeburgi, Tschek.

Members of the genus *Holocremnus* are mainly parasitic on TENTHREDINIDAE, but practically nothing has been written on the biology of *H. ratzeburgi*, and records of its occurrence are few. It has been recorded from :—

Bupalus piniarius ... Germany (Habermehl, 1922).
Diprion pini ... ... Russia (Meier, 1929) ; Germany (Scheidter, 1934).
Diprion polytomum ... Finland (Forsius, 1932) ; Austria (Tschek, 1872).
Trichiosoma lucorum ... Germany (Schmiedeknecht, 1908).
Microcryptus contractus ... Poland (Sitowski, 1925).

This last record, in which Sitowski states that *H. ratzeburgi* is hyperparasitic on *M. contractus*, appears, from a consideration of certain facts in the life-history of both species, to be very unlikely. The egg of *Holocremnus* is laid in the host larva and it develops as an internal parasite inside the spun-up host, while that of *Microcryptus* is laid in the cocoon and it develops as an external parasite. It would therefore be much more likely for the external-feeding *Microcryptus* to destroy the internal-feeding *Holocremnus* than for the latter to destroy the former.

This is one of the three most important larval parasites of *D. polytomum* in Europe. It has invariably been present in every locality in which the sawfly has been collected throughout Bohemia and in Germany. Usually it is present in quite good numbers, from 7 to 20 per cent., contributing a very fair proportion of the parasitism. When in small numbers, 1 to 5 per cent., it is because the total parasitism is low or it has suffered from hyperparasites, or in competition with intrinsically superior parasites (usually cocoon parasites, especially Chalcids). In places where the sawfly host is present in regular numbers it attains its highest parasitism. For example, at Tyssa in 1932 and 1933 it reached 14 per cent. and 17 per cent. ; in the Kunžak and Neu Bistritz areas of South Bohemia in 1932, 2 per cent., 1933, 4 per cent., 1934, 18 per cent., 1935, 20 per cent., 1936, 12 per cent. In the Böhmerwald, where there was a great abundance of the host in 1934, it reached 18 per cent., and in 1935 approximately the same figure. In the highest locality where *D. polytomum* has been found, the Riesengebirge Mountains at 800 metres, it reached 12·0 per cent., a high enough figure considering that parasitism in general was low in this region. Thus in regular abundance it equals *Exenterus* and surpasses *Lamachus*, though the latter has shown higher figures on occasions.

Superficially the adults can at once be recognised from the other parasites of *D. polytomum* by the uniform black matt coloration of the thorax and abdomen, unrelieved by any markings except the yellow tegulae. In contrast to the black body the immaculate red femora stand out conspicuously. The small, quadrate, stalked areolet of the forewing, although sometimes absent, is also distinctive. Of all the subgenera of the old genus *Limneria*, this is the most difficult to recognise, and is easily confused with *Angitia* parasitic on Lepidoptera. The female of *Holocremnus* may be recognised readily from the latter by the shorter ovipositor, never protruding beyond the anus ; the male can only be distinguished by the shape of the head and colour of the abdomen. Length averages 11·5 mm.

H. ratzeburgi is a primary parasite of *D. polytomum*, attacking the fourth and fifth stage larvae, the eggs being laid most usually in the last thoracic or first few abdominal segments, a black puncture mark remaining visible on the skin of the parasitized larva at the site of insertion of the parasite's ovipositor. There must be a backward movement of the parasite's eggs in the body cavity of the larva, as in dissected larvae the majority of eggs and all empty eggshells were found in the posterior abdominal segments. Only a few freshly-laid eggs were found in an anterior position and close to the puncture mark. Such a movement could easily be brought about by the peristalsis of the larval intestine which would tend to push the eggs gradually backwards in the body cavity. Very frequently two eggs are deposited in a larva, and as these are most usually found closely adhering in pairs, it seems likely that they have been laid by one female at the same time. The laying of the eggs does not seem to affect the host larva in the least ; it continues feeding and almost invariably enters the prepupal stage and spins its cocoon before succumbing to the parasite. There must be an interval, the duration of which is uncertain, perhaps one, two, or three weeks, between the laying and the hatching of the eggs to allow for this. Eggs laid in autumn on the second generation of *D. polytomum* invariably overwinter in the hibernating larva and hatch in the following spring. It is by no means unusual for eggs to remain unhatched and the parasitized larvae to recover. On one occasion, four unhatched *Holocremnus* were found in the body cavity of a healthy adult *D. polytomum*. They must have remained in the coelom

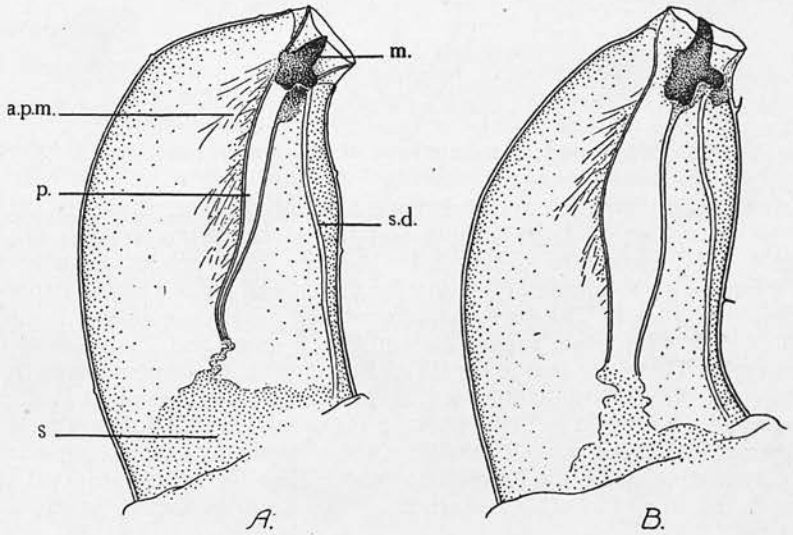

Fig. 11. Head of primary larva of (*A*) *Holocremnus ratzeburgi* ; (*B*) *Lamachus* sp. (both × 200) : *a.p.m*, anterior pharyngeal muscles ; *m*, mandible ; *p*, pharynx ; *s*, stomach ; *s.d*, salivary duct.

throughout the metamorphosis. On comparing parasitism figures based on dissections of larvae with the actual emergence of parasites from similar batches, the former figures were always found to be higher, the most extreme case being 28 per cent. by dissection and 14 per cent. by emergence for the second generation at Tyssa in 1932. The egg (fig. 1*d*) is sub-reniform in shape, from 0·68 to 0·8 mm. in length and 0·23 to 0·26 mm. in breadth, of a dark brown colour, with an exceedingly tough chorion, but showing no sculpturing or markings.

The primary larva (fig. 2*c*) is of typical caudiform shape, cylindrical, with a large strongly chitinized head-capsule, thirteen body segments and a comparatively short tail. After hatching it measures 0·9 mm. in length, the head being 0·27 mm. long and 0·14 mm. broad, and the tail 0·17 mm. long. The skin is uniformly smooth on the body and tail. The head (fig. 11*a*) has a pair of strong, hooked, sharp-pointed mandibles, set just within the buccal cavity, while the pharynx has thick chitinized walls and is strongly muscular for two-thirds of the length of the head. It then leads into the thin-walled stomach. The salivary duct opens into the base of the buccal cavity between the mandibles. There are two pairs of papillae ventrally and three pairs dorsally on the head-capsule. There are no antennae and nothing resembling maxillary or labial structures have been made out.

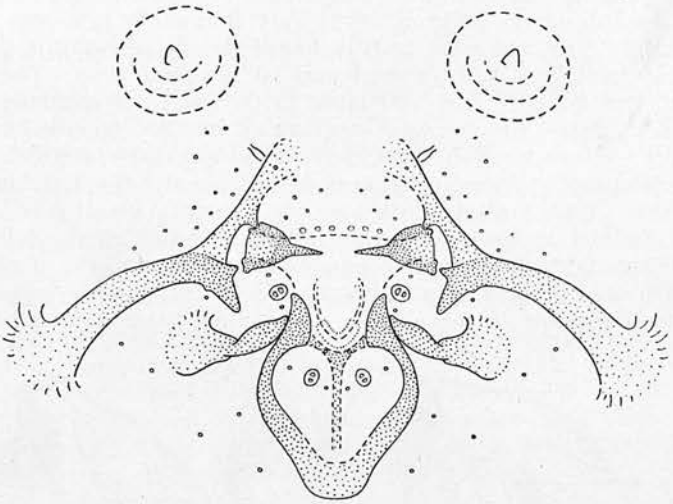

Fig. 12. Mouth-parts of mature larva of *Holocremnus ratzeburgi* (× 80)

The number of larval instars undergone has not been ascertained. At the first ecdysis the characteristic head-capsule and tail of the primary larva are lost. It continues to feed internally and in 8 to 12 days has reached maturity (fig. 4*b*), emerges from the now completely empty host skin, and spins a white, papery cocoon within that of the host. The very characteristic egg-shells are always present in the empty host skin. Pupation takes place in 4 to 5 days, and 2 or 3 days later the adult emerges. There are two generations in the year, corresponding with those of *D. polytomum*. Adults are on the wing in June and July, and again late in August and September. Eggs laid in September, in the second generation larvae of *D. polytomum*, do not hatch at once but remain in the hibernating host prepupa and hatch, and the larvae develop, in the following spring. Thus the length of larval and pupal life is much the same in both generations, being mainly affected by the prevailing temperature.

This being the only Campopleginine among the *D. polytomum* parasites, the larva, with the characteristic head-skeleton (fig. 12) of that group, is very easy to

recognize. The most obvious features characterizing both this species and most of the group, and easily visible in the living larvae, are : the labial ring, the base of which is drawn out or produced ventrally, giving it almost a keyhole shape, distinct from the circular or horseshoe shape amongst the other parasites ; the Y-shaped pigmented superficial area within the labial ring and below the salivary opening, dividing the labium into two distinct lobes ; the greatly reduced maxillary struts and obtuse angle made by hypostoma to pleurostoma ; the labial struts adjoining the upper sector of the labial ring, level with the salivary opening. Besides these there are a number of minor characters distinguishable in a microscopic preparation, the chief being : the incomplete epistoma ; the mandibles with long, pointed teeth, sickle-shaped in lateral view, and without bristles ; the U-shaped salivary opening ; the large number and arrangement of sensillae. The skin structure of *Holocremnus* (fig. 16*h*) is not a very definite feature, nothing like that of the Cryptines or *Exenterus*. The skin is closely covered with small, rather flattened and rounded conical scales. They are less closely packed and more rounded than in the case of *Lamachus*. There are no hairs or setae on the larvae. The spiracles (fig. 15*h*), on the other hand, afford a ready distinction, being unlike those of any other group. They are minute, actually smaller than in the Chalcid parasites of this host, with a simple atrium 0·018 mm. in diameter, surmounting a slightly wider globular chamber, representing the stalk, which leads directly into the tracheal arm, which has to be constricted to receive it. There is no closing apparatus, but the stalk has a number of fine, hair-like processes radiating inwards from its walls. The whole spiracle has the shape of a cottage loaf, and is only just over 0·02 mm. in length. The small size, and absence of a closing apparatus, seem typical features of the spiracles of endoparasitic larvae, being prevalent throughout a number of such larvae that have been examined.

H. ratzeburgi, as one of the most important parasites of *D. polytomum* in Europe adaptable to a wide range of climatic conditions, should have the possibilities of becoming a useful controlling agent in Canada. Its liberation was advised in the first year of the investigation, since when 3,500 have been sent over and liberated in the infested areas, but so far as our information goes, this species has not yet become established under the new conditions.

16. Lamachus sp.

So far as is known, all eleven species of this genus confine themselves to the DIPRIONIDAE for hosts, but only one, *L. spectabilis*, Holmgr., has been recorded as attacking *D. polytomum*. The present species, very close to but distinct from *L. marginatus* of *D. pini*, is possibly new, but this cannot be determined without reference to Ratzeburg's original types and others in the museums in Germany.

This has been found to be one of the commonest larval parasites of *D. polytomum*, coming next to *Exenterus* and *Holocremnus* in abundance, occasionally surpassing both. The normal abundance is from 4 to 10 per cent. ; for example, in 1932 at Tyssa in the Erzegebirge Mountains, 4 per cent. ; in the Brdy Wald, 12 per cent. ; South Bohemia, 8 per cent. ; Tharandt, in Saxony, 6 per cent. ; and the Riesengebirge Mountains, 4 per cent. It is very rarely absent from a locality, though it has occasionally failed, and is usually scarce in the lowest-lying *D. polytomum* grounds in Central Bohemia, such as Dobřiš and the Sazava region. For example, in 1935, Dobřiš (400 m.), 2 per cent. ; Pleše (500 m.), 4 per cent. ; Kunžak (600–700 m.), 8 per cent. ; Silesia (600 m.), 12 per cent. ; Riesengebirge Mountains (800 m.), 10 per cent. In 1936 much the same gradation was observed : Dobřiš, 4 per cent. ; Sazava region (500 m.), 1 per cent. and absent ; Pleše, 9 per cent. ; Kunžak, 8 per cent. ; Silesia, 24 per cent. The highest recorded was 26 per cent. at Kunžak, in the South Bohemian mountains, in 1933. This was the highest figure recorded for any larval parasite.

Lamachus is distinguished among the *D. polytomum* parasites by being a rather large, slender insect, with elongated abdomen, long, thin, curling antennae, very long legs and wings, the areolet of which is very small and triangular. The female is distinctly darker than the male, being of a general blackish colour above, relieved only by yellow tegulae and scutellum and pale yellow edges of the abdominal segments. The face and lower side of the abdomen is bright yellow in fresh specimens. The male has a conspicuous yellow patch mid-dorsally on the third and fourth abdominal segments, and the underside is entirely yellow, from bright to pale lemon. The legs of both sexes are yellow to reddish yellow, with the hind tarsi black and hind tibiae black distally, but with a broad white ring centrally, sometimes extending to the base. This species can be distinguished from *L. marginatus*, which it most closely resembles, by the following characters: In the male, the metapleurae are mostly yellow, instead of black; abdomen conspicuously yellow centrally; hind tibiae much more broadly white; puncturing of mesopleurae less deep and conspicuous, second abdominal segment more strongly coriaceous: in the female the abdominal segments are more strongly sculptured; hind tibiae more conspicuously marked with white; mesopleurae with punctures less distinct. Length, from 11·5 to 13·0 mm.

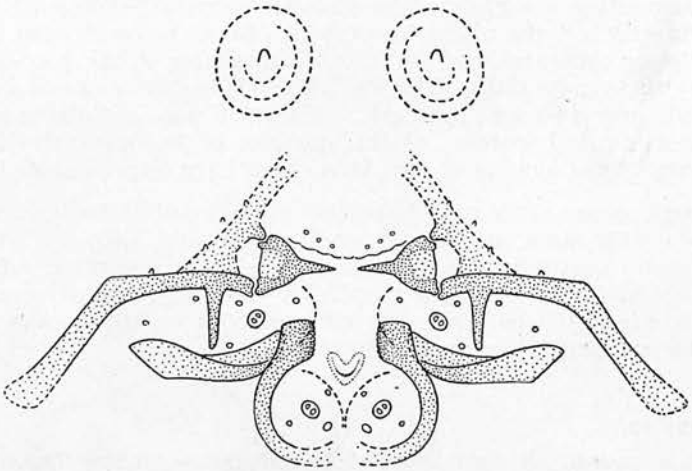

Fig. 13. Mouth-parts of mature larva of *Lamachus* sp. (× 80).

Lamachus is primary and endoparasitic on the larval stages of *D. polytomum*, laying its eggs in the fourth and fifth stage larvae. It is a large egg, from 0·98 to 1·08 mm. long, by 0·3 to 0·36 mm. wide, strongly curved and tapering equally at each end (fig. 1*e*). The chorion is of a dark brown colour and unsculptured. In both size and shape it is easily distinguished from the eggs of *Holocremnus*. The primary larva hatches from a hole at one end of the egg and is of caudiform type. It is slightly larger than that of *H. ratzeburgi*, and may be distinguished from it by the differently formed labial ring and the presence of papillae on the tail, as well as by the size (fig. 11*b*). In length it measures 1·5 mm. × 0·3 mm., the tail being 0·2 mm. long. The head-capsule averages 0·34 mm. long by 0·25 mm. wide. The skin of the thirteen segments is smooth, only the tail bearing papillae. The larva feeds internally until full-grown, when it leaves the perfectly empty host skin and spins a thin white cocoon within the host cocoon. As with *Holocremnus*, the egg-shells are always to be found in the empty host skin. Development rarely proceeds until the host has entered the prepupal stage and spun its cocoon. The period elapsing before the emergence of the adult varies considerably in the first generation, from 10 to 40 days, the average being three weeks. This is bivoltine, as is the host.

The mature larva (fig. 13) has characters quite distinct from those of the other Tryphonine parasites, *Exenterus* spp., but has characters in common with others of the MESOLEPTINAE, which have been examined. Most characteristic is the broken appearance of the labial ring, due to the chitin of the basal sector being much thinner and unpigmented. This is very obvious in the living larva. Other characters of this species are : The elbowed hypostoma ; the short maxillary struts ; the labial struts adjoining the top of the labial ring, above the level of the salivary opening, which itself is rather deeply placed within the labial ring, and distinctly U-shaped ; the labium is divided into two lobes, as in *Holocremnus*, but without the Y-shaped pigmented area between them ; the epistoma is incomplete ; the mandibles are similar to those of *Holocremnus*, with pointed, inwardly curved teeth unarmed with bristles. The skin structure (fig. 16*i*) is similar to that of *Holocremnus*, but the scales are more sharply conical and more closely packed. The spiracle (fig. 15*i*), as in the other endoparasitic larvae, is small and without closing apparatus. The flattened-spherical atrium, a little over 0·02 mm. in diameter, has very faint annular thickenings basally. The thin-walled stalk, slightly annulated apically, leads directly into the tracheal branch without any closing apparatus. The whole spiracle is 0·05 mm. long.

It is evident from the Bohemian records quoted above that this parasite is capable of attaining quite a high degree of control on *D. polytomum* under the right conditions, and its liberation in Canada has been advised from the first. Some 6,850 specimens have been liberated, but it has not yet been recovered from local sawfly hosts. Judging from the distribution in Europe, it is not so suited to a low, dryish climate, but attains its maximum effect in the warm but damp climate of moderately high mountains, between 600 to 800 m., such as the Silesian and South Bohemian ranges.

17. **Lamachus spectabilis,** Holmgr.

This is the only species of *Lamachus* previously recorded as parasitizing *D. polytomum*, in Finland by Forsius (1932). In the present work it has been found mainly as a parasite of *D. abieticolor* in various parts of Bohemia, also bred from *D. sertifer* in the Riesengebirge, and on a very few occasions it has been reared from larvae of *D. polytomum* in the Erzegebirge and the South Bohemian Mountains.

This is distinct from the previous and more abundant species, as an altogether darker insect. The yellow shoulder markings are missing, and on the metathorax the markings are darker and less distinct ; the pale edges of the abdominal segments in the female are much less conspicuous, often so dark as to be hardly differentiated ; in the male the yellow patch on the abdomen is small and duller ; the face is less conspicuously yellow ; in the hind legs, the femora and tibia are mainly black, the white ring on the latter being small and restricted to the basal segment. This is slightly smaller than the previous species, measuring from 10 to 12 mm. in length.

Judging by its prevalence on *D. abieticolor* this might prove a useful parasite of *D. polytomum*, but our knowledge is too scanty to advise upon this point.

18. **Exenterus tricolor,** Roman.

Members of the genus *Exenterus* are parasitic exclusively upon larvae of the DIPRIONIDAE, but this species is one of the least known, having only one previous host record, from *D. polytomum* in Finland (Forsius, 1932). During the present work this species has been bred from *D. polytomum* mainly in the Erzegebirge and Riesengebirge Mountains, on both the Saxon and Bohemian sides, and once from South Bohemia. It has also been obtained in a few instances from *D. sertifer* in the Riesengebirge, and two specimens from this host in Sweden. Thus its distribution corresponds always with the more mountainous, colder, and wetter regions in which the host is

found, in contrast to the next species, *E. adspersus*, which occurs all over the lower regions of Bohemia. It is capable of attaining quite an abundance. At Tyssa in 1932, 19 per cent. of *D. polytomum* larvae of the first generation were destroyed by this parasite, and 17 per cent. of the second generation. In Saxony in the same year it accounted for 11 per cent. and 8·5 per cent. of the first and second generations respectively. Since then its numbers at Tyssa have declined somewhat, there being at the same time an increase in another larval parasite, *Holocremnus ratzeburgi*. In 1933 only 10 per cent. of larvae were destroyed, in 1934 this had fallen to 3 per cent. In the Riesengebirge, where only a single generation of the host occurs in a year, the percentage parasitism by this species was always low, from 2 to 4 per cent. *E. tricolor* was also bred in small numbers from *D. sertifer* in the Riesengebirge in 1933 and 1934.

The species of this genus are extremely difficult to separate owing to the range of individual variation. Morley (1911) describes fifteen species as British, but on the Continent Schmiedeknecht (1911) states that of the seven species described only two can be distinguished with certainty, the remainder being colour variants of these. Thomson (1883 and 1889), however, gives fairly clear descriptions, making the separation of 6 species possible. The identification of our species has been based on these descriptions. Among the parasites of *D. polytomum*, *Exenterus* can be distinguished by the absence of tibial spines on the hind legs. Beyond this it can be recognized at once as a handsome black insect with conspicuous yellow markings on the body and legs. The hind margins of the abdominal tergites are typically banded with yellow. The three species of *Exenterus* occurring on *D. polytomum* are by no means easy to separate from one another and from other members of the genus. *E. tricolor* is fairly easily recognized by the apical segments of the abdomen being ventrally and sometimes laterally of a reddish colour. In the female the last abdominal sternite is long and acute instead of broad and obtuse as in the other species. The face, legs, and underside of the thorax are more widely marked with yellow than in the other species, the front and middle legs being entirely yellow with the exception of the femora, which are marked with black, sometimes only a black spot. *E. marginatorius* can be distinguished from both these species, and from the other species in the genus except *E. abruptorius*, by the well-marked ridge or keel along the anterior margin of the mesosternum. From *E. abruptorius*, which it most closely resembles, it can be separated by the claws in the female being not pectinate. *E. adspersus* can be distinguished from *E. marginatorius*, apart from the above character, by the finer punctation of the thorax, and by the greater amount of yellow on the front legs, the coxae and femora only being marked with black, while in *E. marginatorius* the femora and tibiae are strongly black above and yellow below. Further than this, *E. marginatorius* is markedly larger and stouter, with the markings more strongly developed, especially the yellow banding of the abdominal tergites being much broader on the first two segments. *E. tricolor* and *E. adspersus* are smaller and more slender, with the yellow markings, especially on the abdominal tergites, less pronounced. *E. tricolor* averages 6·8 mm. in length.

Regarding the biology of *E. tricolor*, adults have been captured early in June, flying round the sunny margins of spruce plantations, and again in September and even mid-October. These late records are of adults captured round wire cages where numbers of second generation larvae were being reared to maturity. It has been found to correspond with the host in its life-history, having two generations in most of Bohemia and a single generation in the Riesengebirge. The eggs are laid externally on the larva of *D. polytomum*, most commonly on the dorsal or lateral aspect of the thoracic segments, though occasionally far back on the body or attached to a leg. Larvae thus affected show no traces of having been stung by the parasite. Oviposition is on the fourth or fifth stage larvae or prepupae, the mature larvae being most often attacked. Hatching does not occur until after the spinning of the host cocoon, and the parasite larva feeds externally on the prepupa within the

cocoon. It will be seen, then, that the host goes through one or two ecdyses between the oviposition and hatching of the parasite, and this necessitates a special modification of the egg in order that it shall not be lost during these moults.

The egg (fig. 1*c*) is yellowish-white in colour and covered with a scale-like sculpturing, of an elongated pear-shape, the narrow end tapering acutely with the chorion prolonged into a short stalk. This stalk is embedded in a dark-coloured, hard, button-shaped disc, of quite a different substance from the chorion. The egg averages 0·5 mm. long by 0·18 mm. at the widest point ; the stalk is 0·05 mm. long and the dark disc 0·06 mm. in diameter. The stalk penetrates the skin of the sawfly larva and the disc lies under the skin embedded in the muscle layer, with its diameter at right angles to the stalk. Thus the disc acts as an anchor, and so firm is this attachment that, under natural conditions, 80 to 90 per cent. of the eggs survive the one or two subsequent moults of the host larva. This is possible because of the elasticity of the freshly shed skin, the *Exenterus* egg either pulling through the tiny hole in the skin at the point of attachment, or a small piece of skin breaking away and remaining round the base of the stalk, leaving a jagged hole in the old skin, through which the egg easily slips. If the moult is prolonged or difficult, or in a dry atmosphere, the egg is much more likely to be torn from its anchorage and lost with the cast skin. In just under 50 per cent. of a number of cases kept under observation in a laboratory the eggs were lost on ecdysis in this way, but such heavy losses were probably due to the dry atmosphere in the rearing glasses. The dependence on humidity for the survival of the eggs must have an important bearing on the distribution and success of this parasite in the field, and this will be discussed later. Even after the egg has come through the ecdysis, it is subject to much mechanical action during spinning, when there is great danger of its being knocked off by the coarse resinous threads of the cocoon inside which the prepupae is actively turning. Hatching occurs in from 5 to 15 days in the first generation, but in 10 days to a month in the autumn. It is of the greatest importance to the parasite that hatching should not take place until the cocoon is formed, otherwise the young larva is invariably lost in the ecdysis or spinning and is unable to regain the newly moulted host.

The newly hatched larva (fig. 2*b*) is of a dull white colour, bluntly fusiform in shape, 0·55 mm. long and 0·23 mm. wide. The head is well chitinized and bears a pair of strong, curved mandibles and a pair of small antennae. The body, of 13 segments, has a lateral armature of long, strong hairs, almost 0·1 mm. in length, giving the primary larva a very characteristic hairy appearance, easily visible without a lens, by which it can be readily distinguished from those of all the other parasites. The base of the hairs, especially the larger ones, is apparently muscular, as they have a limited power of movement. The arrangement of the hairs can be seen from the illustration. The last segment has a pair of caudal bristles or setae, which probably function in retaining a hold on the egg-shell when the larva is hatching. Under high magnification, the cuticle can be seen to be covered with small slender setae, similar to those of the full-grown larva (*q.v.*). By means of these setae and hairs, the primary larva can move about in a very active manner when necessary. The larva hatches from the outer pole of the egg and immediately fixes itself by flexing the body until the head reaches the skin of the host and a grip can be obtained with the mandibles. For an hour or two it remains in this position with the tail still retaining a hold in the egg-shell, doubtless by means of the caudal bristles. After it has fed for this short while, the hold by the tail is released, and during the rest of the first stadium it remains fixed to the host by the mandibles alone, never relaxing its hold or altering its position unless accidentally knocked off. In this eventuality it can move about actively, and soon regains its hold upon the host. During this time the host is still living, but soon after the first moult of the parasite larva it is found to be dead. The exact point at which death occurs and the reason are not clear. On the first ecdysis the parasite loses its long motile hairs, but still has a skin armature of minute fine setae. It now becomes

more active and does not remain fixed to the host but moves about, feeding at different positions. Should more than one *Exenterus* egg be laid the young larvae will feed together during the first stadium, but during the second stadium one invariably predominates and kills and devours the others. In the first or summer generation there is now an intensive feeding period, the larva passing through five stadia, to become full-grown in a little over a week from the time of hatching. The mature larva now spins a semi-transparent, whitish, papery cocoon, excluding the completely empty and shrivelled host remains, and enters the prepupal stage. This lasts five days to a week in the first generation, 3 to 6 days as an eonymph, and one to three days as a pronymph. In the second generation the larva usually completes its feeding before the onset of cold weather and passes the winter in the eonymphal stage, appearing only in the following spring. Occasionally larvae of the second generation go into hibernation in the second or third instars and complete their development in the following year. As might be expected, this is of more frequent occurrence in the colder regions. Pupation occurs shortly after the assumption of the pronymphal stage in both generations, being preceded by defaecation and ecdysis. The pupa libera is at first clear white in colour, only the eyes being dark red. It darkens rapidly and in 4 to 5 days the adult emerges.

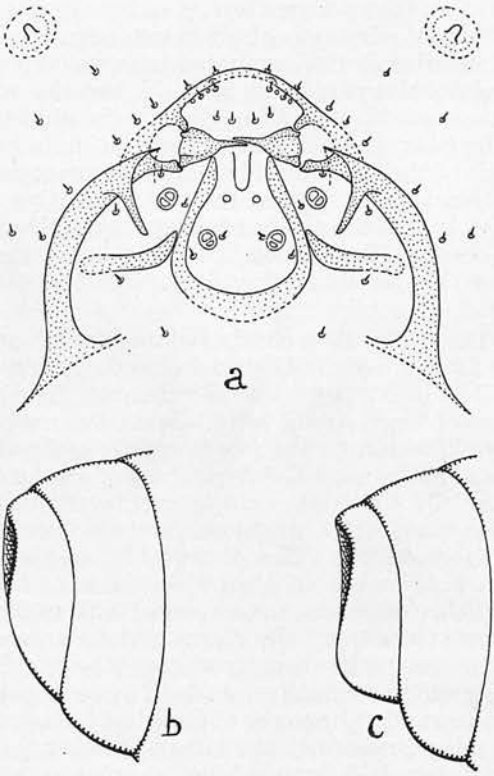

Fig. 14. *a*, mouth-parts of mature larva of *Exenterus tricolor* (× 80) ; *b*, last abdominal segment of *Exenterus adspersus* ; *c*, last abdominal segment of *Exenterus* sp.

The mature larva of *E. tricolor* (fig. 4*c*), shining creamy-white in colour, 6 mm. long by 2·7 mm. broad, does not differ, on casual inspection, from the other parasites, except that it is considerably smaller than *Microcryptus*, *Holocremnus*, *Lamachus*, and *Pimpla*. Under the microscope the distinctive features of the head and skin are

easily distinguished. The chitinous head appendages (fig. 14*a*) are not only smaller but also more compact than those of the four above-mentioned genera. It lacks the clypeal arch, chitinized salivary opening and ligula of the Cryptines. The complete, horseshoe-shaped labial ring of approximately equal width throughout distinguishes it from *Holocremnus*, *Lamachus*, and the Pimplines. Further distinctive characters are the rather slender mandibles with long sharp points without any bristles, the complete epistoma, the well-developed, curved hypostoma, not widely separated basally; the labial struts adjoining the labial ring nearly mid-way between base and apex. The skin armature of *Exenterus* (fig. 16*g*) is very characteristic, consisting of a number of fine, slender setae, 0·024 mm. in length, with rather swollen, rounded bases set in slightly sunken pits in the cuticle. They are closely arranged all over the body segments, and even in the living larva, under comparatively low magnification, they impart a distinctive, slightly downy appearance to its skin.

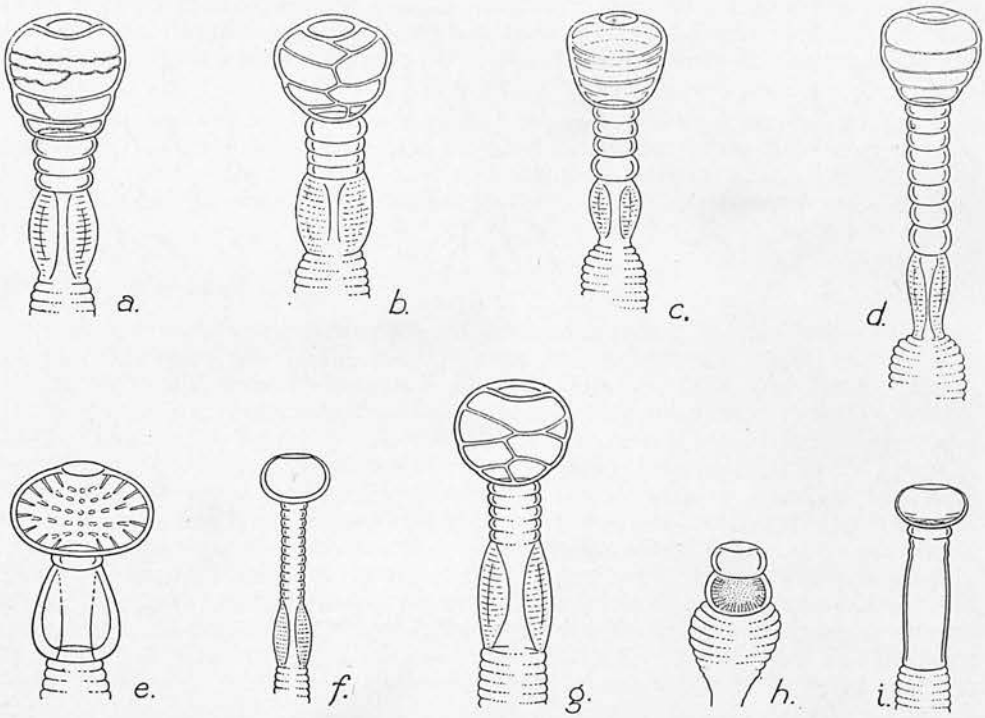

Fig. 15. Spiracles of (*a*) *Microcryptus basizonius*; (*b*) *Spilocryptus abbreviator*; (*c*) *Habrocryptus polytomi*; (*d*) *Hemiteles areator*; (*e*) *Pimpla alternans*; (*f*) *Delomerista* sp.; (*g*) *Exenterus tricolor*; (*h*) *Holocremnus ratzeburgi*; (*i*) *Lamachus* sp. (all × 450).

The spiracle (fig. 15*g*) also affords a useful distinctive character. The atrium, almost spherical, 0·035 mm. in diameter, flattened on top, has a fine, reticulate thickening to the inner surface. A short annularly thickened stalk leads into the thick-walled closing apparatus. The whole spiracle is 0·08 mm. long. No attempt has yet been made to distinguish between the larval stages of the four species of *Exenterus* found on *D. polytomum* (mainly through lack of time), but small differences do exist and it is hoped they may be described later. The above description of *E. tricolor*, however, is distinctive of the larvae of these four species and serves to separate them from those of other genera.

Exenterus tricolor, and the other species also, have one extrinsic disadvantage, which seriously impairs their efficiency. It has been pointed out that the survival of the eggs is dependent on a high atmospheric humidity, enabling them to come through the last one or two moults of the host, and that larvae hatching too soon invariably perish. In the laboratory, 50 per cent. losses were incurred in this way because of the low humidity, but the loss in the field is probably much lower, less than 20 per cent. This will inevitably lessen the parasite's efficiency and chances of its becoming a very important controlling agent. Another effect is on the distribution of the parasite. It would be expected to attain its maximum efficiency in regions of high humidity or heavy rainfall. Actually this species has only been found in the wet mountainous regions of Bohemia and Northern Europe. Here it is capable of attaining a fairly high parasitism, but it is significant that this was highest (at Tyssa) in 1932, a year of heavy rainfall, and the rate fell off very sharply in the following years, when the rainfall was considerably below normal. Its only appearance in

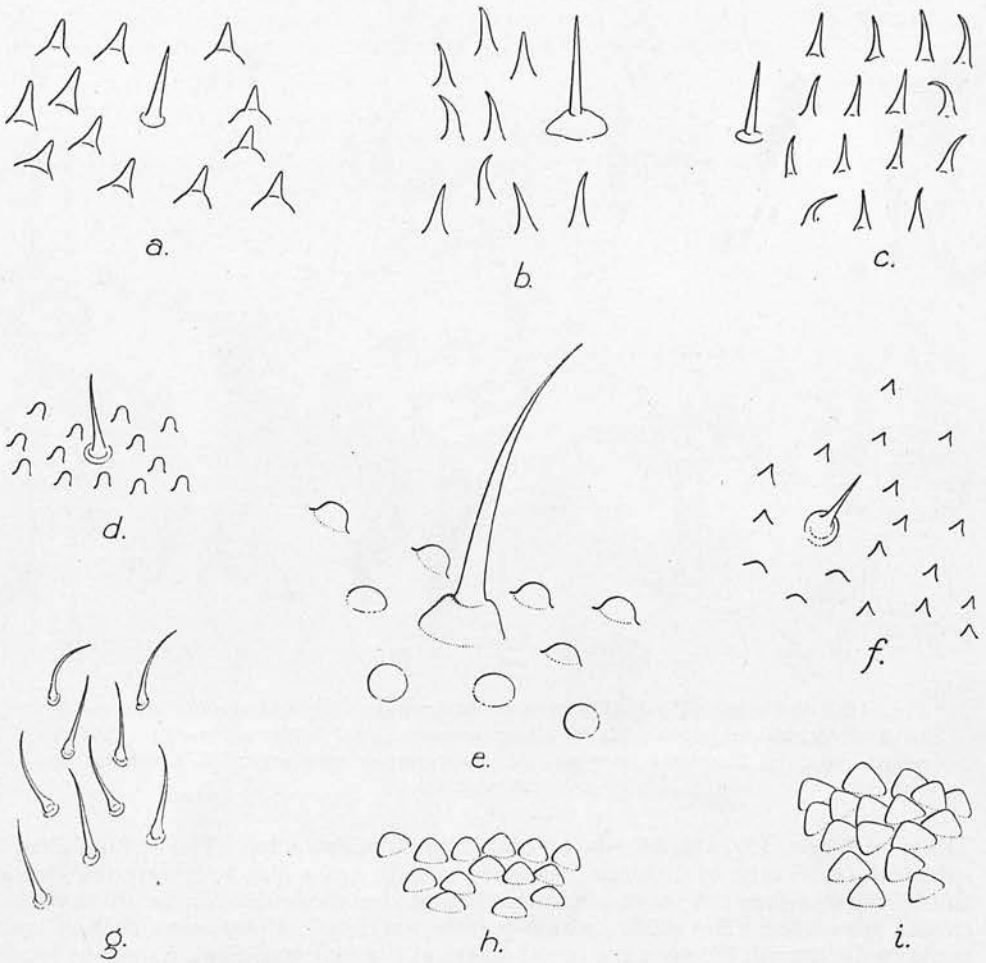

Fig. 16. Skin armature of (*a*) *Microcryptus basizonius*; (*b*) *Spilocryptus abbreviator*; (*c*) *Habrocryptus polytomi*; (*d*) *Hemiteles areator*; (*e*) *Delomerista* sp.; (*f*) *Pimpla alternans*; (*g*) *Exenterus tricolor*; (*h*) *Holocremnus ratzeburgi*; (*i*) *Lamachus* sp. (all × 450).

South Bohemia was in 1936, a year of exceptionally heavy rainfall (see Table, page 376). It is interesting to compare *E. tricolor* with *E. adspersus*, which latter has the same oviposition habits and therefore disadvantages, but is distributed over the lower (and drier) regions of Central and Southern Bohemia and Silesia. When the figures are comparable, *i.e.*, in the same season and from localities with a fair abundance of *D. polytomum*, *E. adspersus* has never shown so high a parasitism as *E. tricolor*. For example, in 1932: *E. tricolor*—Tyssa, 19 and 17 per cent., Tharandt, 11 and 8·5 per cent.; *E. adspersus*—Brdy Wald, 5·5 per cent., South Bohemia, 2 and 3 per cent. This latter species remained at about the same level, 3 to 5 per cent., in subsequent years, and only in 1936 (the very wet year) did it attain anything like the abundance shown by *E. tricolor*. Comparison in this year was impossible, as sufficient numbers of *D. polytomum* were not obtainable from the localities where *E. tricolor* was present. Evidently low humidity of the habitat acts as a severe check on both these species, more especially in the case of *E. adspersus*. In this case there is every chance of these parasites attaining their maximum efficiency in the wet mountain regions of the Gaspé Peninsula, or the coastal districts of New Brunswick. Such a marked climate preference should certainly be studied in making liberations.

E. tricolor was liberated in Canada in the first year of the work, but has not yet been recovered. This should by no means be taken as evidence of its unsuitability, since it has not yet been sent over in very great numbers, and the chances of its having already attained appreciable abundance at the points of liberation are consequently small.

19. Exenterus adspersus, Htg.

This is a fairly common parasite of the pine sawflies, having been bred from *D. pini* in France (de Gaulle, 1908), Russia (Meier, 1927 and 1929), and Finland (Hertz, 1933) and from *D. sertifer* in Bavaria (Jemiller, 1894) and Russia (Meier, 1927). It has also been bred on one occasion from *D. polytomum* in Finland (Forsius, 1932). During the present work it has been the commonest species of *Exenterus* parasitizing *D. polytomum*, being of more frequent occurrence than *E. tricolor*, because of its wider distribution, though the latter seems to attain greater local abundance, as has been pointed out above. It is of very widespread and regular occurrence throughout Czechoslovakia, being found in practically every sample of *D. polytomum* from every locality except the Riesengebirge. It occurs most frequently at the lower and middle altitudes where the host is found, and is rarest in the north of Bohemia, the Erzegebirge, where *E. tricolor* is most abundant. It is usually present in from 3 to 5 per cent. of the host larvae, but under favourable conditions has been found infesting as much as 13 per cent. Its incidence seems to depend largely on the prevailing climatic conditions, as will be discussed later. A single specimen of *E. adspersus* was bred from *D. sertifer* in the Riesengebirge in 1933.

The distinctive characters of the adults are set out in the section on *E. tricolor*. It is a rather larger species than the above, averaging 7·5 mm. in length, and has a stronger, less slender appearance, somewhat darker, with the yellow markings on legs and abdomen less conspicuous. The biology is in every way similar to that of *E. tricolor*, no differences having yet been observed, and the larval stages of the two species have not yet been distinguished. Consequently, it suffers from the same intrinsic disadvantage in that the eggs have to come through one or two ecdyses of the host in order that the parasite may survive. As has been pointed out in the case of *E. tricolor*, a fairly high atmospheric humidity is absolutely essential in order that a large proportion of the eggs may survive; consequently, it is to be expected that the distribution of such an insect and its seasonal abundance will be influenced mainly by humidity or rainfall. In the case of *E. adspersus* the distribution, for reasons not yet understood, is generally over the lower and middle heights of Czechoslovakia,

not in the highest and wettest regions, as might be expected. Consequently, the influence of seasonal rainfall is, if anything, accentuated. This is very well demonstrated by the following sets of figures, showing the percentage of *E. adspersus* on *D. polytomum* in different localities and different years, the rainfall in mm. (the figure in brackets) being given for the six months May to September of each year. This is the important period of the year when *Exenterus* is active and subject to the influence of climate.

Table showing Incidence of E. adsperus *on* D. polytomum, *and Rainfall, in mm., for May to September.*

Locality	Brdy Wald	Hradec in Silesia	South Bohemia
Height in metres ...	400	600	550–700
1932	(423 mm.) 5·5%	—	(372 mm.) 8·1%
1933	(244 mm.) 5·0%	—	(347 mm.) 8·0%
1934	(254 mm.) 2·1%	—	(338 mm.) 4·2%
1935	(267 mm.) 2·5%	(449 mm.) 4·7%	(305 mm.) 4·0%
1936	(410 mm.) 6·0%	(547 mm.) 13·0%	(374 mm.) 10·0%

Not only does the abundance in each locality vary regularly with the summer rainfall, but it is also significant that on comparing the three localities, the higher the rainfall the greater is the incidence of *Exenterus*. It must be borne in mind that the picture is by no means a simple relationship of *E. adsperus* with climate ; many complicating factors are involved, the most important being the fact that the host is also favoured by a high humidity, and as there is always a lag between the increase of host and parasite, the true effect of rainfall on the parasite will always be damped down somewhat. There can be no doubt, then, that an abundant rainfall is definitely advantageous to the increase of this parasite. As has been pointed out in dealing with the previous species, this makes *E. adspersus* particularly suitable for liberation in parts of the Canadian infestation with an especially moist climate. Numbers of this species, totalling approximately four thousand, have been liberated every year since 1933, and the first recoveries were made in 1934. This and subsequent recoveries leaves no doubt as to the ability of *E. adspersus* to adapt itself to Canadian conditions, and it should prove to be a valuable component of the parasite complex that we hope will eventually be established.

20. Exenterus marginatorius, F.

This common larval parasite of the pine sawflies has only occurred in one isolated instance on *D. polytomum* in South Bohemia, though small numbers have been bred from *D. sertifer* in Czechoslovakia and in Sweden, and also from *D. virens* and *D. pallidum* in Czechoslovakia.

The adults of *E. marginatorius* are larger, stronger, and more striking looking than those of *E. tricolor* or *E. adspersus*. In size it averages 8·8 mm. long. The distinctions from the other species are detailed in the section on *E. tricolor*.

Scheidter (1934) gives a good description of the oviposition of this species on *D. pini*. As with the other members of the genus, oviposition is on the larvae or prepupae and development takes place within the host cocoon. We have not had sufficient numbers of this species to enable us to make a description or distinction of the larval characters.

There is no reason why *E. marginatorius* should not be introduced into Canada, if it could be obtained in sufficient quantity in Europe. The larger size of the Canadian race of *D. polytomum* and the different conditions might enable it to multiply with success upon this host.

21. Exenterus sp.

Recently a fourth species of *Exenterus* has been bred from *D. polytomum* closely resembling *E. adspersus*, but with certain features which definitely separate it from the others as a distinct species. It has not yet been possible to name this, but it is perhaps a new species. It has only been recognized in the most recent year, 1936. It is quite probable that it has always been present and has been confused with *E. adspersus*, especially considering the fairly wide distribution and good numbers recovered, but in this year the host, *D. polytomum*, was collected and studied in far greater numbers than had ever been done before, and this would tend to show up the less common parasites. It occurred in greatest numbers at the lowest altitudes and became progressively rarer in the higher regions. As *D. polytomum* is present in numbers in these low regions only in exceptionally wet years, such as 1936, this again might explain the previous absence of this species. The localities where it was recovered were: Sazava region (360 m.) 14 per cent.; Dobříš in the Brdy Wald (400 m.) 3 per cent.; Pleše, South Bohemia (500 m.) 5 per cent.; Neu Bistritz, South Bohemia (550 m.) 5 per cent.; Hradec, Silesia (600 m.) 1 per cent.

The adults of this species of *Exenterus* resemble *E. adspersus* very closely in every respect—size, colour, markings, etc.—and are only to be recognized on the following characters, of which the shape of the last segment in the female is the most distinctive:—

Exenterus adspersus	*Exenterus* sp.
Last abdominal segment of female broadly convex (fig. 14*b*).	Last abdominal segment of female right-angled (fig. 14*c*).
Front and middle coxae black, yellow beneath, tarsi yellow, hind coxae black.	Mid coxae almost or entirely yellow, hind coxae yellow, black above.
Propodeon less conspicuously yellow marked.	Propodeon more conspicuously yellow marked.

Nothing is yet known of the biology of this species, except that it is a primary larval parasite of *D. polytomum* developing within the cocoon, but its close resemblance to *E. adspersus* would lead one to expect their life-histories to be similar. In distribution it seems to occupy an even lower region than *E. adspersus*, just as *E. adspersus* is distributed at a lower altitude than *E. tricolor*, there being, of course, considerable overlapping. Further details of its biology and relationships with the other members of the genus will be of very great interest, and it is hoped that it will soon be possible to supply them. Meanwhile, there need be no fear as to the advisability of liberating this undoubtedly primary parasite into Canada; indeed, it has probably already been liberated in some numbers.

22. Microbracon sp.

Only one specimen of this unidentified species of *Microbracon* was bred from a second generation cocoon collected at Zbiroh, Central Bohemia, in 1932.

23. Monodontomerus dentipes, Dlm.

This Chalcid has been recorded from a number of Hymenopterous and Lepidopterous hosts, frequently as a secondary on various Ichneumonids and Braconids. It can, however, act as a primary parasite on pine sawflies, having been bred from *D. pini*, L., in Holland (Ritzema Bos, 1919) and Germany (Scheidter, 1934) and from *D. pini* and *D. similis* in Poland by Sitowski (1929), and from *Diprion* spp. in Poland by Mokrzecki (1933). Sitowski observes that it may often be hyperparasitic. It already occurs in North America, where it was observed by Weiss (1917) to be heavily parasitizing *D. similis* in New Jersey in 1916, and subsequently proved to be one of the most effective checks upon this species in New Jersey and Pennsylvania (Hartley, 1923).

This is probably one of the most important parasites of *D. polytomum* in Europe, and it has been found with regularity in cocoons from every locality in Czechoslovakia, frequently in quite high proportions. It is difficult to estimate the percentage reached by such cocoon parasites, firstly because a large number of cocoons have not always been obtainable from each locality ; secondly, because the generations of these small Chalcids by no means synchronize with those of the host ; they are constantly emerging and ovipositing in new cocoons, so that the amount of destruction is cumulative from the time the first *Diprion* cocoons appear. The proportion of cocoons parasitized will depend entirely on when they were collected. Collections made soon after spinning have shown an entirely different parasitism from those made shortly before emergence. Even a big sample taken throughout the time cocoons are available will necessarily underestimate the effect of such parasites. When sufficient numbers of such cocoons have been collected, *M. dentipes* has always been present, the percentage varying from 4 or 5 to 40 per cent. The abundance varies tremendously from year to year, and there is no indication of preference for certain terrains as in many of the other parasites. Frequently, when *Eutelus subfumatus* is abundant, *M. dentipes* will be comparatively rare, and *vice versa*. The importance it can attain is shown by a few figures : Brdy Wald area, 1932, 22 per cent., 1933, 35 per cent., 1934, 16 per cent., 1935, 9 per cent., 1936, 6 per cent. ; South Bohemia area, 1933, 28 per cent., 1934, 18 per cent., 1936, 10 per cent. During these investigations *M. dentipes* has been bred from *D. pallidum* in Bohemia, but never from *D. pini* or *D. sertifer*.

This species is characteristic among the Chalcid parasites of *D. polytomum*, as the only one with a long, exserted ovipositor. It is a large, dark species, the head, thorax, and abdomen having a dark, metallic greenish-blue sheen. The hind coxae are very large, three times as large as the others, with a strong, blunt tooth on the posterior edge distally, and the femora are also broad and strong, and with a well developed tooth distally. The wings are faintly clouded with brown and the stigmal area has a distinct dark brown patch. The stigmal vein is very short, much shorter than the postmarginal. The ovipositor is exserted and almost as long as the abdomen. Length 2·75 to 3·5 mm. Ovipositor 1·0 mm.

This has always been found as a primary parasite on *D. polytomum*, although in view of the records, it is quite possible that it may occasionally act as a secondary. It is a parasite of the prepupal stage, a female laying always more than one egg, usually 5 or 6, in the sawfly cocoon. Fifteen eggs have been found in a single cocoon. The egg (fig. 17*a*) is very large for such a small insect, being 0·7 mm. long by 0·2 mm. broad, glossy white in colour and covered with symmetrical rows of minute spicules. In shape it tapers abruptly at the broader end, rather gradually at the other end towards the micropyle, a slight knob. The life-history of *M. dentipes* has not been fully worked out ; all attempts to breed it in captivity have failed, probably because there is a fairly long period, a month or two, between the emergence of the adults and their sexual maturity. In repeated experiments these parasites have neither copulated nor shown any inclination for oviposition in the three or four weeks they have survived in captivity, whereas the other common Chalcids, *Microplectron*, *Dibrachys*, and *Eutelus*, have all copulated and oviposited soon after emergence.

The larvae of *M. dentipes* feed externally on the prepupae, which they consume completely. The average number of adults emerging from a cocoon is 4·5, but as many as 12 have been reared from a single host. It has a fairly slow development for a Chalcid. Larvae have been found to take 3 to 4 weeks to reach maturity, and the pupal period has been found to last 3 weeks in early spring, though it may be shorter in summer. Hibernation takes place in the prepupal stage inside the host cocoon, pupation occurring in April and the first adults emerging in May. Adults have been found on the wing throughout every month in summer and into late September. This may be due to a long length of life, but is also due to the fact that

all the members of one brood do not by any means emerge at one time ; a full month has been found to elapse between the emergence of the first and last insects from one cocoon, and it very frequently happens that some larvae of late broods pupate and adults emerge in autumn, while others in the same cocoon go into hibernation and the adults appear in the following spring. Because of the slow development and the

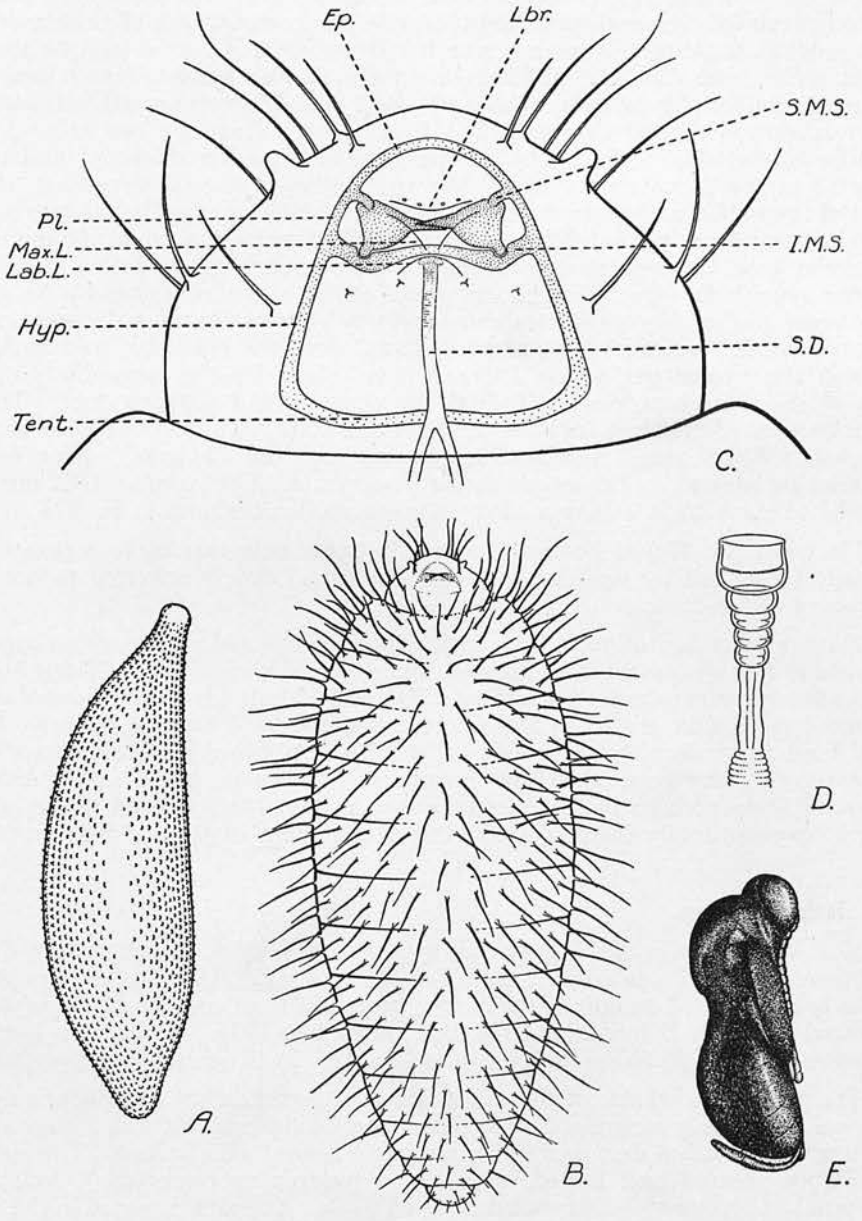

Fig. 17. *Monodontomerus dentipes*: (*a*) egg (× 90) ; (*b*) mature larva (× 25) ; (*c*) head of mature larva (× 150) ; (*d*) spiracle (× 450) ; (*e*) pupa (× 12·5) ; *Ep*, epistoma ; *Hyp*, hypostoma ; *I.M.S*, inferior mandibular strut; *Lab*, labium ; *Lbr*, labrum ; *Max.L*, maxillary lobe ; *Pl*, pleurostoma ; *S.D*, salivary duct ; *S.M.S*, superior mandibular strut ; *Tent*, tentorium.

time taken in reaching maturity there are probably only two generations in the year, with a great deal of overlapping, but with favourable weather, such as a warm and early spring and late autumn, there is the possibility of a third generation.

The larvae of this species can be distinguished from those of all the other parasites by their very hairy appearance, easily visible to the naked eye, and apparent even in the first stadium. The full grown larva (fig. 17*b*), consisting of a head and 13 body segments, is semi-translucent, creamy white in colour and thickly covered with long white hairs, 0·3 mm. in length. It measures 3·5 mm. long by 2·0 mm. broad. The head (fig. 17*c*), 0·5 mm. in width, is also furnished with long hairs arranged in a definite pattern. There are also a pair of short, papilla-like antennae, and a labrum behind which opens the salivary duct. There are two pairs of setose papillae on the labial region. The internal head skeleton has the same fundamental basis as in the Ichneumonid larva, but is simpler. The well developed, sharply pointed mandibles articulate on the superior and inferior mandibular struts. The superior strut bears the condyle which fits into a fossa on the top of the mandible's triangular base, the lowest angle of which bears a condyle fitting into a fossa on the inferior mandibular strut. The superior and inferior struts are joined by the pleurostoma and the inferior struts are continuous below the pharyngeal opening. The pleurostoma is continued forward to form an arch, the epistoma, and backwards to form the hypostoma, whose lower end is joined by the inwardly projecting arch of the tentorium, passing behind the pharynx and salivary duct. The two branches of the latter fuse together at about this point. This type of head structure is constant, with small modifications, throughout the Chalcids. Nine pairs of spiracles are present, in the second to tenth segments. The atrium is 0·02 mm. wide and the whole spiracle 0·04 mm. long, the construction is shown in fig. 17*d*.

The pupa (fig. 17*e*) at first pale yellow, but gradually turning to a glossy black, is easily recognised by the long recurved ovipositor, closely adhering to the dorsal surface of the abdomen.

There was no hesitation in introducing into the infested areas such an important parasite of *D. polytomum* with a proved ability to acclimatise itself in North America. In the first year of parasite liberations, 1933, 13,731 individuals of this species were liberated in Canada, a part of these coming from Europe but the majority having been bred from *D. similis* cocoons collected in Ontario. Increasing numbers of these insects have been sent from Europe in subsequent years, and it has been recovered from cocoons in the infested areas, so that there is good reason to hope that it may eventually develop into an important enemy of *D. polytomum* in Canada.

24. Habrocytus sp.

Most of the species of this genus are hyperparasitic upon a large variety of hosts, and there seem to be no records from TENTHREDINIDAE. During the present work it has been obtained on only three or four occasions from cocoons of *D. polytomum*, collected in South Bohemia and the Böhmerwald in 1934. It has also been bred from cocoons of *D. pallidum* from the same locality. In all cases it was hyperparasitic.

The present knowledge of this group does not permit of the identification of this species. It is easily recognized among the other Chalcid parasites as a large species, 3·5 mm. long, with a dark metallic green lustre tinged with bronze. The abdomen is sharply pointed and keeled, with the ovipositor not exserted. Occiput not carinated. Clypeus with four well-developed teeth. Antennae inserted in the middle of the face, ten-jointed. Tarsi five-jointed, hind tibia with only one spur. Wings clear, with marginal vein shorter than subcostal and postmarginal longer than stigmal.

It is obvious that such a hyperparasite would be very undesirable in Canada.

25. Eutelus subfumatus, Ratz.

This Chalcid has been previously recorded from *D. pini* (Cameron, 1889) and *D. sertifer* (de Gaulle, 1919) in France. It ranks with *Monodontomerus dentipes* as one of the most important parasites of *D. polytomum* in Europe. It has occurred with regularity in every locality in Czechoslovakia, very frequently in abundance. The difficulty of estimating the true rôle played by such a cocoon parasite has already been pointed out, but, considering the high parasitism occasionally recorded, the accumulated effect of *E. subfumatus* must prove a very important check on the increase of *D. polytomum*. In 1936 fairly large collections of cocoons were made from most of the collecting localities in Bohemia, and from the figures obtained,

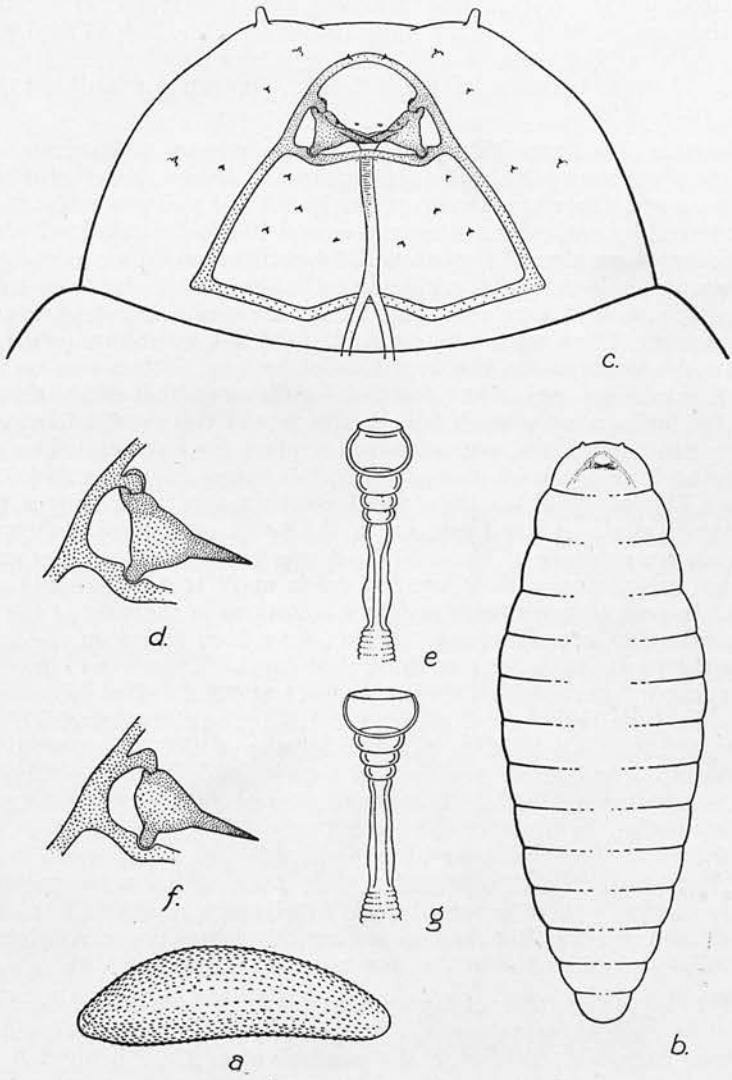

Fig. 18. *Eutelus subfumatus*: (*a*) egg (× 90); (*b*) mature larva (× 25); (*c*) head of mature larva (× 150); (*d*) mandible (× 450); (*e*) spiracle (× 450); (*f*) mandible of *Dibrachys cavus* (× 450); (*g*) spiracle of *D. cavus* (× 450).

which are quite representative, an idea of the importance of this parasite can be gathered:—Dobříš, 5 per cent., Sazava region, two localities, 9 and 13 per cent., Kunžak and Pleše, South Bohemia, 12 and 20 per cent. respectively; Silesia, 23 per cent. It always appeared in special abundance in the Erzegebirge and the South Bohemian Mountains. Here a 30 per cent. parasitism has been recorded several times, and occasionally, from small samples of cocoons collected late in the season, as many as 60 per cent. have produced *Eutelus*. This parasite has also been bred from *D. pini* and *D. pallidum* in Bohemia.

Eutelus subfumatus may be distinguished among the Chalcid parasites of *D. polytomum* by the brilliant metallic green colour of the head, thorax and abdomen, and the bright yellow legs and antennae, the latter tipped with brown. The occiput is not carinated and the clypeus does not bear a median tooth. The antennae are inserted at the base of the face, below a line drawn from the base of the eyes. Wings clear, with the marginal vein shorter than subcostal, and stigmal shorter than postmarginal. Length between 1·0 and 2·5 mm., depending mainly on the number emerging from a cocoon.

E. subfumatus is a primary parasite of *D. polytomum*, ovipositing within the cocoons on the prepupa or pupa. The egg (fig. 18*a*), 0·45 mm. long by 0·13 mm. wide, is somewhat curved, tapering sharply at the broad end and gradually at the other. In shape it resembles a gherkin. It is white, and the surface studded with minute, round tubercles. A number of eggs are laid by each female in a cocoon, from 3 or 4 up to 30, the average being 10. On hatching, the larvae feed on the host prepupa or pupa, killing it after a day or two, and finally devouring it completely if enough larvae are present. There are five active stadia, the last, or mature larval, gradually merging into the prepupal on the cessation of feeding. After two or three days as a prepupa, in summer, pupation takes place, and in a further two or three days the adults emerge, biting a very small hole in the side of the cocoon. In autumn the prepupae go into hibernation, pupation taking place next spring. The number of adults emerging from a cocoon averages 9·5, but frequently from 20 to 25 survive and emerge. The length of the life-cycle depends mainly upon temperature in the localities investigated. At midsummer in the lower regions of Bohemia, with a monthly mean temperature of 18 to 20°C., it was three weeks. Later in the year, or in the high mountains, with a monthly mean of 11 to 15°C., it was five weeks. It was found to pass through three or four generations in the year at the lower and warmer altitudes in Central Europe. Adults have been found on the wing in the Erzegebirge Mountains in Saxony at the end of April. These would have an opportunity of laying in unemerged *Diprion* cocoons at once. The second generation emerges late in June, when some cocoons of the first generation of *D. polytomum* are already present. The third generation, because of the higher temperatures in July, emerges at the end of this month or in August, while there are still late cocoons of the first generation available. The fourth generation does not emerge until the middle of September, in time for the second generation host cocoons. The insect passes the winter in the mature larval or prepupal stage, going into hibernation in late September. Naturally the successive generations are by no means so clear cut as the above picture; there is considerable overlapping owing to late emergences, etc., and cold and wet weather may so prolong development and shorten the flight and oviposition periods as to cut out a generation altogether.

The mature larva (fig. 18*b*), of typical Chalcid form, is rather elongate, 3·0 mm. long by 1·0 mm. wide, tapering posteriorly from the widest part in segments 4 and 5, and somewhat narrowed anteriorly, the hemispherical head being 0·5 mm. wide at the base. It is yellowish white in colour, glistening and semi-transparent, with a perfectly smooth cuticle, only a few minute papillae being discernible under high magnification. The glossy-white head (fig. 18*c*) shows three lobes, two epicranial, bearing the antennae, and one labial, below the mouth. The labrum is obtusely

pointed, and bears two pairs of sensillae, marginally. There is also a definite arrangement of spicules on raised, swollen bases, the distribution on the anterior aspect of the head being characteristic, and shown in the illustration. The head skeleton is of the usual Chalcid type, described above under *Monodontomerus dentipes*, only the general shape and lay out, and the relative proportion of the components to one another, afford distinctive characters useful for separating the different species. The larva of *Eutelus* can be distinguished at once from that of *Monodontomerus* by the absence of hairs, but it is not easy to separate from those of the other Chalcids, especially from the hyperparasite *Dibrachys cavus*. It can be distinguished from *Microplectron* by the different arrangement of spicules on the head ; also by the narrower, more rounded epistoma and the different shape of the mandibles (fig. 18*d*), and of the spiracles (fig. 18*e*). Practically the only distinctions from *D. cavus* lie in the shape of the mandibles and spiracles. Such minute differences can only be discerned in a good preparation under the microscope. They are difficult to describe and can be best appreciated from a study of the illustrations. The mandible of *E. subfumatus* appears somewhat larger and stronger than that of the other two, and the base is produced into a flange above and behind the fossa of the upper articulation, this flange appearing behind the superior mandibular strut when the whole head skeleton is undisturbed, and being very easily spotted if the mandible be removed. The point of the mandible appears to be more slender and sharper in *D. cavus*. The superior mandibular strut seems longer in this species, and more distinctly right-angled than in *E. subfumatus*. Also the pleurostoma appears stronger and thicker. The spiracles are much the same in size and structure, only the atrium appears more globular in the case of *Eutelus*, with a slightly smaller opening. In each case there are three distinct globular chambers below the atrium ; below the third the top of the stalk itself is swollen, almost making a fourth chamber. The lower part of the stalk develops into a longish, thick-walled swelling, the closing apparatus, below which it suddenly widens out to join the trachea. The atrium is 0·02 mm. in diameter and the whole spiracle is 0·06 mm. long. In *D. cavus* the atrium is 0·023 mm. in diameter.

This is probably one of the most valuable parasites of *D. polytomum* in Europe and its establishment in Canada would be a step of great importance. Its liberation has been advised from the first and 11,500 individuals have been sent from Europe and liberated by 1936.

26. Dibrachys cavus, Walk.

This notorious hyperparasite has been recorded from a long range of Lepidopterous, Hymenopterous, Dipterous and Coleopterous hosts. It is, unfortunately, all too frequently present on *D. polytomum* in Europe, although it has been found acting as both primary and secondary on this host. It has rarely been absent from any sample of cocoons and shows an impartial distribution all over Czechoslovakia. The parasitism is rarely less than 3 or 4 per cent., frequently up to 8 or 10 per cent. of cocoons, though higher figures have not been recorded.

The adults can be distinguished among the other Chalcids as a small dark species, almost black in colour with a metallic blue sheen on the body. The legs and antennae vary from pale to dark brown. The head is markedly carinate, and the antennae inserted fairly low down on the face, but not below the level of the base of the eyes. The abdomen is flattened and longish oval in shape. The wings are clear, with the costal longer than the marginal veins and the post-marginal and stigmal veins equal in length. The size varies from 1·5 to 2·75 mm. in length, depending on the number emerging from a cocoon.

This species is most usually secondary on *D. polytomum*, though it quite often acts in a primary capacity. It attacks practically any of the primary parasites, remains of the larvae of *Exenterus*, *Microcryptus basizonius*, *Lamachus*, *Holocremnus*

ratzeburgi, and *Hemiteles areator*, having been found in *D. polytomum* cocoons from which *D. cavus* emerged, and of *Torocampus eques* and *Pimpla alternans* in cocoons of *D. sertifer*. A number of eggs are laid in each cocoon, and up to 40 adults have emerged from a single cocoon, though 12 to 15 is the average. The larvae feed externally on the parasite or sawfly prepupa, devouring it completely. The life-cycle is completed in three weeks in summer, with the temperature averaging about 20°C. As parasitized cocoons are available for a longer period in the field than unparasitized, owing to the slower development of the parasite, *D. cavus* can practically always find hosts available from its first appearance in May to its hibernation, as mature larvae, late in September. Thus it can go through 3 or 4 generations in the year in Central Europe.

The mature larva is very similar to that of *Eutelus subfumatus* and the very slight differences in mandibles and spiracles have been described in the section on that parasite and illustrated in figures 18*f* and *g*.

For the sake of the biological control project as a whole, it is to be hoped that this dangerous hyperparasite does not appear in the infested areas in Canada. Its quick life-cycle and fecundity give it a reproductive rate considerably above that of any of the larval parasites it chiefly victimises. In our experience, whole generations of *Holocremnus* and *Lamachus* have been wiped out by hyperparasitism by this species, together with *Hemiteles* and *Leptocryptus*. Dissected sawfly larvae had shown a 10 to 20 per cent. parasitism by larval parasites, whereas cocoons from the same batches produced no adults of these species. It is true that in such cases the total loss of the host through parasitism remains the same, but the effect on slowing down the rate of increase of the primary parasites is obvious.

27. Diglochys lophyrorum, Rshka.

The original description of this species by Ruschka and Fulmek (1915) is the only previous record. On this occasion it was bred from *D. pini* cocoons in Bohemia, but the authors do not state whether it was primary or secondary. It was bred from *D. polytomum* cocoons on three or four occasions only during the present work, never more than one or two cocoons in a sample containing this parasite, the percentage being well below 1 per cent.

It is a small, dark insect, most easily confused with *Dibrachys cavus*, being of the same size and colour. The body is dark metallic green, the antennae and legs yellowish brown to dark brown. *Diglochys* can be distinguished from *Dibrachys* by the shape of the abdomen, which is much shorter and round (roundish-oval in male) in contrast to the long, oval abdomen of the latter. The head is large and broad, wider than the thorax, and weakly carinate. Mandibles 4-toothed on each side. The wings are clear, with the marginal vein slightly shorter than the subcostal, and the postmarginal equal to the stigmal.

This species was of too infrequent occurrence for anything definite to be learned of its biology. Judging by the remains in cocoons from which it emerged, it can act as both primary and secondary parasite on *D. polytomum*, and until more information is forthcoming it would be unwise to attempt its introduction into Canada.

28. Stenomalus sp.

From a second generation cocoon of *D. polytomum*, collected at Zbiroh, Central Bohemia, in 1932, a dead adult female of an unidentified species of *Stenomalus* was dissected out.

29. Pleurotropis sp.

This is recorded as a hyperparasite of various Agromyzid, Coleopterous, and Hymenopterous hosts. One or two isolated examples were bred from *D. polytomum*

cocoons from the Brdy Wald and Böhmerwald areas. It is a small, dark metallic green insect, distinguishable from the other parasites by the following points: abdomen relatively small and oval, tarsi 4-segmented, wings clear with very short subcostal vein, broken before joining the long marginal vein, very short radial vein, postmarginal only slightly larger.

Nothing is known of the biology of this Chalcid, except that it is hyperparasitic in the present instance, and for this reason it should be withheld from liberation in Canada.

30. **Microplectron fuscipennis,** Zett.

The biology and importance of *M. fuscipennis* have already been fully dealt with in a previous paper (Morris & Cameron, 1935) and only our more recent observations, together with the repetition of a few important points, will be given here.

During the first three years of the work, this species was not found parasitizing *D. polytomum,* though widely distributed on *D. pini* and *D. sertifier* throughout Europe, becoming a major parasite of *D. sertifer* in the south. The reasons put forward to explain this were: (1) the solitary habits and comparative rarity of *D. polytomum,* which might prevent this parasite from attaining appreciable numbers; (2) the comparative small number of host cocoons that had been collected in the field and examined. In 1935 *M. fuscipennis* was recovered in small numbers (the exact percentage was not ascertained) from cocoons of the first generation of *D. polytomum* collected at Padrt in the Brdy Wald; in 1936, cocoons of this species collected late in the first generation at Hradec in Silesia yielded 12 per cent. of this parasite. In these two years very much larger numbers of cocoons were gathered than at any time previously.

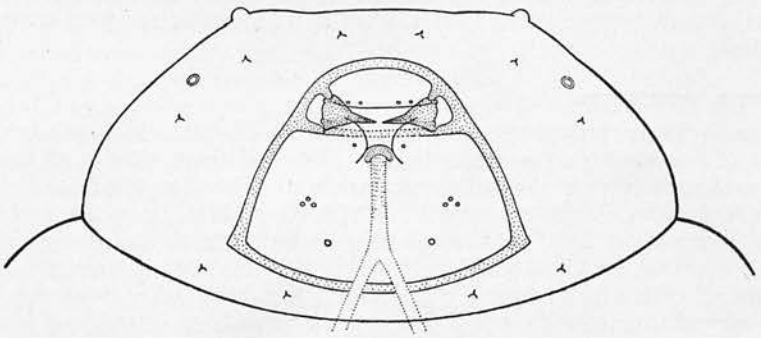

Fig. 19. *Microplectron fuscipennis*: head of mature larva (× 150).

The adults of *M. fuscipennis* are conspicuous because of their dark, clouded wings; general black colour with greenish tinge on head and thorax, and polished bronze abdomen; contrasting white legs; and the marked sexual dimorphism. This latter character is most apparent in the antennae, those of the male being branched, of the female club-shaped. Besides this, the male is smaller, the wings are less clouded, the coxae dark brown, and the abdomen longish oval instead of rotund. The fore-wings of both species are clouded with brown over two-thirds of the distal area with the basal one-third clear. The hind wings are clear. The subcostal and marginal veins are about equal, and the radial longer than the postmarginal.

As with *D. sertifer,* this is really a primary parasite of the sawfly, though occasionally found acting as a secondary on one or other of the Ichneumonid primary parasites. This hyperparasitism was studied in greater detail in the case of *D. sertifer,*

and it was considered to be accidental, being really an aspect of multiple parasitism in which the Chalcid was invariably intrinsically superior to the Ichneumonid. The only difference in the biology observed with *D. polytomum* as a host was the smaller number of eggs laid and of adults emerging from the much smaller cocoons of this sawfly. In Silesia the average number of adults per cocoon was only 12. On *D. sertifer* this was found to be 31 in Hungary and 72 in Jugoslavia.

The immature stages are fully described and illustrated in the paper (*loc. cit.*). The eggs can be distinguished from those of *Eutelus*, *Dibrachys*, or *Monodontomerus* by their small size, being only 0·34 mm. by 0·11 mm. The distinctions of the mature larvae of these four species have been mentioned in the section on *Eutelus*. It is only necessary to repeat here the main features of *Microplectron* (fig. 19) : the small mandibles without an upper basal flange, the broad epistoma, and the grouping of the papillae, especially the pair of very large conspicuous papillae lateral to the mouth-parts and in line with the superior mandibular struts, and the two groups of three together on the sub-labial region.

When *M. fuscipennis* was first discovered in numbers parasitizing *D. sertifer* in Hungary in 1934, its value was at once realized and its liberation in Canada advised, and in that year cocoons containing an estimated nine millions of this parasite were sent from Europe. During that winter mass breeding on *D. polytomum* cocoons was started at Farnham House Laboratory, and in the following year this was adopted in the Laboratory at Belleville, and has since been carried on, with the production and liberation of nearly twenty million *Microplectron*, besides which further large shipments of naturally infected *D. sertifer* cocoons have been sent from Europe. The chances of *Microplectron* becoming a really useful controlling factor of *D. polytomum* in Canada are considered pretty good, depending on its tremendous fecundity and rapid rate of increase and the presence of large quantities of readily available host material. The fact that the first recoveries of the insect from Canadian cocoons collected in the field were made in the winter of 1934, only six months after the first liberations, and that it is now well established in many localities, lend strong support to this view.

31. Sturmia inconspicua, Meig.

This exceedingly polyphagous Tachinid seems to attack Lepidopterous and Tenthredinid hosts with equal impartiality. Besides many species of Lepidoptera, it has been recorded from the following sawflies : *Diprion frutetorum*, *D. laricis*, *D. pallidum*, *D. pini*, *D. polytomum*, *D. sertifer*, *D. similis*, *D. socius*, and *D. virens*. Baer (1920) records it as a parasite of *D. polytomum* in Germany and gives some interesting notes on its life-history. Sitowski (1925) records it from the same host, among other DIPRIONIDAE, from Poland ; and Webber (1932) gives a full account of the biology of this parasite, which has several times been introduced from Europe into the United States for the control of the Gipsy Moth and *Diprion simile*.

During the present work it was obtained in very small numbers (usually less than 1 per cent. parasitism) from *D. polytomum* at Tharandt in Saxony, Tyssa in the Erzegebirge, and Dobřiš in the Brdy Wald. From *D. sertifer*, however, it was obtained in far greater numbers, showing a 65 per cent. parasitism at Wiener Neustadt in 1934, approximately 5 per cent. at Iszák in Hungary in the same year, and a slightly higher parasitism in the Riesengebirge in 1933 and 1934. In Poland it was common on *D. pini*, reaching 20 to 30 per cent. in 1935 and 1936. A full account and figures of the various stages in the life-history of *Sturmia* will not be given here, as it has been so admirably described by Webber. The following notes, mainly from field observations, are given as being useful for the detection of this parasite and for an understanding of its relationship with its host.

The egg is laid externally on the sawfly larva or prepupa, usually on the side of the thoracic region, and the young larva hatches at once and burrows into its host,

where it remains as an internal parasite until fully fed. It then bores a hole out of the empty host skin and pupates within an hour, usually on the ground, lightly buried in the soil or dust, but sometimes on a branch in the neighbourhood of the empty host cocoon. The adults emerge in 3 to 4 weeks. The completion of feeding and emergence of the fully fed *Sturmia* larva takes place, in the majority of cases, after the host has spun its cocoon, but quite often from the dead host larva which has failed in its last ecdysis and spinning. This seems to depend entirely on the age of the larva when it is parasitized. Cocoons from which a *Sturmia* larva has emerged are very easy to recognize, because of the very regular, perfectly round, cleanly cut hole situated exactly at the apex, never slightly eccentric or with jagged edges, as is usually the case with Ichneumonid parasites. The hole is considerably smaller than that made by the emergence of adult sawflies, and slightly smaller than that of most Ichneumonids. Within the cocoon the host skin remains fully distended but completely empty and with a large round hole at one end, most usually posteriorly.

In Central Europe it is usual for *Sturmia inconspicua* to go through several generations in the year. The early generations in spring and summer undergo their development as just described, *i.e.*, the complete life-cycle occupies 5 or 6 weeks. In the last generation in late summer or autumn, however, the primary larva, as soon as it has entered the host, goes into diapause and passes the winter thus, within the sawfly prepupa in its cocoon. In the following spring it devours its host, emerges and pupates within a very short time, and the adults are on the wing in time for the first generation of *Diprion* larvae. A case has occurred, however, in which a *Sturmia* grub, laid on a *D. sertifer* larva in May 1934, went into diapause straight away and did not complete its development or emerge until April 1935. The majority of *Sturmia* of the same generation and from the same host had emerged and pupated in the normal way and given rise to adults in June. These latter must have had alternate hosts, since *D. sertifer* is univoltine. There was a certain number of *D. pini* (bivoltine) in the same infestation and these were heavily parasitized by *Sturmia*, but this host would be no use to the flies emerging in June, as the second generation larvae of *D. pini* were first found in this locality in the middle of August. It seems then that some other hosts, probably Lepidopterous, are necessary for the maintenance of such a strain of *Sturmia*. It is interesting to speculate whether the single generation *Sturmia*, going into diapause as a primary larva in May, is an adaptation to its univoltine host; and whether the presence of the primary larva within the sawfly prepupa inhibits the latter's metamorphosis in September (the emergence time for *D. sertifer*) in order to make this method of overwintering possible. Alternatively, it is possible that the rate of development of the parasite is influenced by that of its host, and that the only *Sturmia* larvae that will survive are those in the small proportion of *D. sertifer* larvae that go into diapause over the winter.

In considering the chances of survival of this species in Canada it must be realized that the biology of *D. polytomum* there is slightly different. Over a very large portion of the infested area in the Gaspé Peninsula, the sawfly is univoltine, with a very prolonged feeding period, from about June to August. At slightly lower levels there are two generations almost merged into one, through prolongation of the first generation's feeding period and irregular emergence of adults. Only on the lowest ground, in New Brunswick, are there two very distinct generations. Thus the requisite conditions do prevail in which *Sturmia* could find an almost continuous supply of hosts through the short summer. The Gaspé would be the best area for liberation of the races from *D. sertifer*. The lower areas would perhaps be more suitable for those coming from *D. pini* and *D. polytomum* in Europe. In parts of Poland, where the winter climate is very severe, *S. inconspicua* is undoubtedly a major controlling agent on bivoltine *D. pini*, so there are the opportunities and possibilities of its becoming an important check on *D. polytomum* in Canada. The ability for acclimatisation has already been proved by its recovery from indigenous cocoons in Canada.

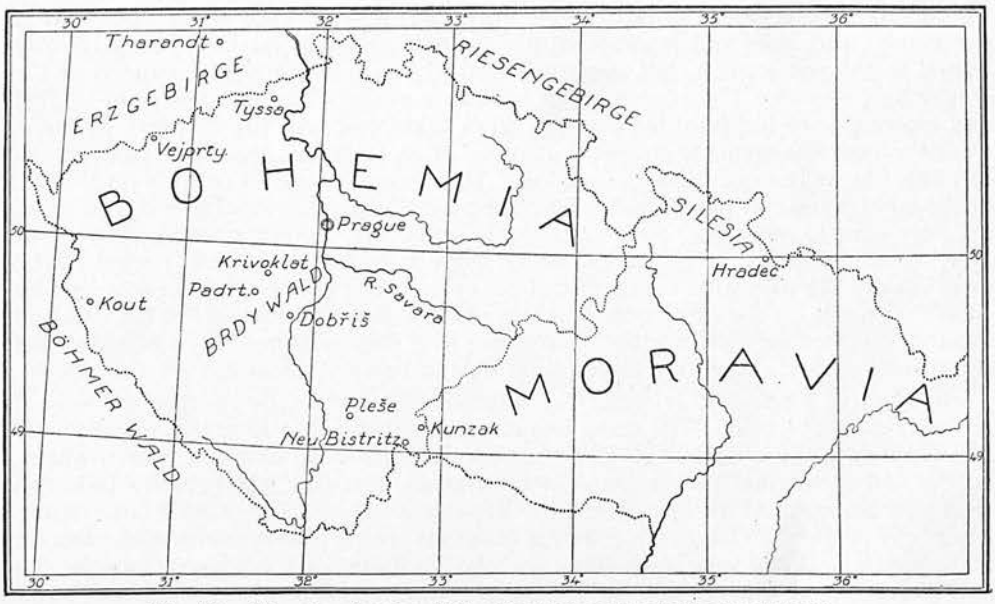

Fig. 20. Map showing the chief collecting centres in Czechoslovakia.

32. Key to the Parasites of Dipron polytomum.

1.—Dipterous ..... *Sturmia inconspicua.*
Hymenopterous 2

2.—Wingless 3
Winged 4

3.—Species 4·3 mm. or longer, excluding ovipositor ; head black, thorax and first three abdominal segments red..... *Gelis acarorum.*
Species only 3 mm. long ; head and abdomen, except for first segment, black ; thorax reddish-brown with metanotum black, petiole light brown... *Gelis* sp.

4.—Wings rudimentary, not extending beyond the metathorax..... *Spilocryptus abbreviator.*
Wings fully developed..... 5

5.—Wings with well-developed venation, antennae not elbowed..... 6
Wings with rudimentary venation, antennae elbowed..... 22

6.—Wings with one recurrent nervure..... *Microbracon* sp.
Wings with two recurrent nervures..... 7

7.—Forewings with three transverse dusky areas..... *Hemiteles areator.*
Forewings without transverse dusky areas..... 8

8.—Hind tibiae without spurs..... 9
Hind tibiae with spurs..... 12

9.—Keel on front margin of mesosternum ; first two abdominal segments broadly banded with yellow..... *Exenterus marginatorius.*
Not as above..... 10

10.—Apical segments of abdomen ventrally red ; last ventral segment in ♀ long and acute ; front and middle legs yellow, only femora marked with black..... *Exenterus tricolor.*
Apical segments of abdomen ventrally not red ; last ventral segment of ♀ obtuse ; front tibiae usually marked with fuscous..... 11

11.—Front and mid coxae black, yellow beneath ; yellow tarsi ; hind coxae black ; propodeon less conspicuously yellow marked ; last abdominal segment in female very obtusely angled (fig. 13*b*).....*Exenterus adspersus.*

Mid coxae almost or entirely yellow, hind coxae yellow, black above ; propodeon more conspicuously yellow marked ; last abdominal segment in ♀ almost right-angled (fig. 13*c*).....*Exenterus* sp.

12.—Areolet present, well defined but with outer side wanting.....13

Areolet present or entirely wanting ; when present always closed.....14

13.—Ridges of metathoracic areolation strong ; abdomen entirely black.....
Hemiteles sordipes.

Ridges of metathoracic areolation weak ; abdomen almost yellowish-red, except for petiole and sides of segments 2 and 3, which are black.....
Leptocryptus aereus.

14.—Areolet distinctly pentagonal.....15

Areolet quadrate, triangular, or wanting.....16

15.—Body entirely black ; antennae black, usually with white spot in middle segments above.....*Habrocryptus polytomi.*

Middle segments of abdomen red, white ring in middle of antennae.....
Microcryptus basizonius.

16.—Abdomen dorsally depressed and broadly sessile ; areolet small and quadrate ; ♀ with ovipositor at least one-third length of abdomen.....17

Abdomen petiolate ; areolet triangular, quadrate or wanting.....18

17.—Metathoracic areolation absent, only vestiges of the two long ; ovipositor only one-third length of abdomen.....*Pimpla* (*Itoplectis*) *alternans.*

Metathoracic areolation partly developed, with completely enclosed area superomedia and area posteriomedia ; ovipositor only half length of abdomen .....*Delomerista* sp.

18.—Areolet large and quadrate, thorax and abdomen shining and slender.....19

Areolet small, quadrate, triangular, or wanting ; thorax matt.....20

19.—Head, thorax, and abdomen mainly black, except for reddish spot in centre of thorax and median segments of abdomen light brown.....
Mesochorus thoracicus.

Head, thorax and abdomen entirely light reddish-brown *Mesochorus fulgurans.*

20.—Areolet small, usually distinctly quadrate, rarely almost triangular ; thorax and abdomen dull black ; tegulae only yellow.....*Holocremnus ratzeburgi.*

Areolet wanting or small and triangular ; face and thorax beneath yellow, black above, with front edge of scutellum and tegulae yellow.....21

21.—Face of ♀ entirely yellow, or with large yellow patch ; hind femora red, tibiae distally black and tarsi entirely black ; abdominal segments with light posterior margin.....*Lamachus* sp.

Face of ♀ usually black, or with small yellow patch ; hind legs, except for coxa, black, or clouded with black ; posterior margins to abdominal segments less markedly light ; only ♀ obtained.....*Lamachus spectabilis.*

22.—Female with exserted ovipositor.....*Monodontomerus dentipes.*

Female without exserted ovipositor.....23

23.—Wings distinctly clouded with dark brown ; antennae of ♀ spindle-shaped, of ♂ filiform with three short branches from segments 2, 3, and 4 of flagellum.....
Microplectron fuscipennis.

Wings clear, antennae of ♂ and ♀ similar.....24

24.—Tarsi 4-segmented ; marginal nerve longer than subcostal.....*Pleurotropis* sp.

Tarsi 5-segmented ; marginal nerve shorter than subcostal.....25

25.—Postmarginal vein of same length as stigmal (radial) ; occiput carinated.....26

Postmarginal vein longer than stigmal ; occiput never carinated.....27

26.—Occiput markedly carinated ; abdomen longish oval.....*Dibrachys cavus.*

Occiput weakly carinated ; abdomen round, in ♂ round oval.....
Diglochys lophyrorum.

27.—Antennae inserted at base of face (below an imaginary line drawn from base of eyes) ; clypeus without median tooth at apex.....*Eutelus subfumatus.*

Antennae not inserted at base of face ; clypeus at apex armed with a median tooth or with four equally well-developed teeth.....28

28.—First joint of antennae not longer than pedicel ; clypeus with four well-developed teeth ; abdomen sharply pointed and keeled ; a large species, dark metallic green tinged with bronze.....*Habrocytus* sp.

Pedicel much longer than any antennal joint ; clypeus at apex with median tooth .....*Stenomalus* sp.

33. Key to the Mature Larvae of the Primary Parasites.

1.—Dipterous larvae emerging from host cocoon before pupation.....
Sturmia inconspicua.

Hymenopterous larvae pupating in host cocoon.....2

2.—Large larvae between 4 and 9 mm. long, Ichneumonid-type head skeleton ; usually solitary.....3

Small larvae, less than 4 mm. long ; Chalcid-type head skeleton ; usually gregarious 11

3.—Labial ring broken basally ; hypostoma elbowed ; spiracles small, atrium 0·02 mm. diameter, and without closing apparatus ; large dark-brown eggs, 1 mm. long, always found in host skin.....*Lamachus* spp.

Labial ring complete ; hypostoma regularly curved or wanting ; spiracles large and with closing apparatus, atrium more than 0·02 mm. diameter, except in *Holocremnus* and *Delomerista* ; eggs not found in host skin, except *Holocremnus*.....4

4.—Labial ring drawn out ventrally, giving it a keyhole shape ; Y-shaped pigmented area in labial ring divides lower part into two lobes ; spiracles minute, loaf-shaped, at most 0·025 mm. long, no closing apparatus ; dark brown egg 0·8 mm. long, always found in host skin.....*Holocremnus ratzeburgi.*

Labial ring horseshoe-shaped, at most thickened basally ; labial area not divided by pigmented Y-shaped strip ; spiracles at least 0·06 mm. long or longer, with closing apparatus ; eggs not found in host skin.....5

5.—Hypostoma wanting ; labial struts mere vestiges ; labial ring with broad, thickened, rather flattened base ; spiracles with broad atrium, 0·045 mm. wide, lined with inwardly projecting spines ; no cocoon spun.....
Pimpla alternans.

Hypostoma present ; labial struts developed ; spiracles with atrium less than 0·04 mm. wide with no internal projections ; white papery cocoon spun...6

6.—Slightly hairy appearance, through hairs 0·1 mm. long sparsely scattered on body ; labial ring thickened and flattened basally, labial struts somewhat reduced ; spiracles small, atrium 0·02 mm. diameter.....*Delomerista* sp.

Larva of smooth appearance ; if spiracles present never more than 0·035 mm. long ; labial ring not flattened or markedly thickened basally ; labial struts well developed ; spiracles large, atrium at least 0·03 mm. diameter . . 7

7.—Clypeal arch absent; epistoma complete; mandibles small, slender pointed, without bristles; ligula absent; salivary opening unchitinized; skin closely covered with fine slender setae, 0·024 mm. long, giving downy appearance under low power.....*Exenterus* spp.

Clypeal arch present; epistoma usually incomplete; mandibles broadly triangular, armed with bristles; ligula present; salivary opening usually chitinized; skin covered with very small papillae or spinules and occasional stiff setae 8

8.—Clypeal arch rounded; epistoma almost complete; labial struts right-angled; spiracle with reticulate thickening to atrium.....*Spilocryptus abbreviator.*

Clypeal arch flattened; epistoma distinctly incomplete; labial struts only slightly curved; spiracles with annular thickening to atrium 9

9.—Opening to salivary duct strongly chitinized; mandibles with broad strong points; spiracles with very short stalk; skin armed with blunt, conical spinules.....*Microcryptus basizonius.*

Opening to salivary duct very weakly chitinized; mandibles with rather more slender points; spiracles with long stalk.....10

10.—Epistoma hardly developed at all; ligula small, V-shaped; spiracle of average size, 0·07 mm. long; skin armed with slender, sharply conical spinules..... *Habrocryptus polytomi.*

Epistoma slightly developed; ligula large, Y-shaped; spiracle with very long stalk, total length 0·1 mm., skin with small, rounded papillae..... *Hemiteles* spp.

11.—Larvae hairy; pupa of female with long ovipositor recurved over back; egg-shells 0·7 mm. long present in cocoon.....*Monodontomerus dentipes.*

Larvae smooth; pupae without projecting ovipositor; egg-shells in cocoon 0·45 mm. long or less.....12

12.—Epistoma broad and flattened; tentorium uniformly curved dorsally; a pair of large papillae on face, one each side of mouth in line with superior mandibular struts; eggs 0·34 mm. long.....*Microplectron fuscipennis.*

Epistoma narrow and rounded; tentorium abruptly arched dorsally in the middle; papillae on face all small and of equal size; eggs 0·45 mm. long...13

13.—Base of mandibles with flange above and behind superior fossa; spiracle with more globular atrium, approximately 0·02 mm. diameter..... *Eutelus subfumatus.*

Mandibles without any basal flange; spiracle with atrium rather flattened, approximately 0·023 mm. diameter, with larger opening.....*Dibrachys cavus.*

34. Summary.

A severe outbreak of the Spruce Sawfly (*Diprion polytomum*, Htg.) in Eastern Canada led to a request to Farnham House Laboratory to investigate, and if possible collect and export, the parasites of this insect in its native home in Europe.

Work started in 1932 and it was found that *D. polytomum* was a comparatively rare insect in Europe, though widely distributed. It is heavily parasitized, 31 species of Hymenopterous and Dipterous parasites having been found up to the present. Nearly twenty-eight million parasitized cocoons and eggs of this and other species of *Diprion* have been collected and despatched from Europe, and work is still continuing.

Previous to the present work only 13 species of parasites, a list of which is given, were recorded from this host.

Of the 31 species now known, 15 are primary, 5 can be primary or secondary, and 9 secondary only ; in 2 cases the status is not known.

Descriptions of all the species are given and in the case of the obligatory and facultative primaries, the biology and immature stages are also described and notes added on their suitability for introduction into Canada. A key to the adult parasites is given, and a key to the larval stages of the primary and facultative primary parasites. Some practical notes are also given, including methods of accelerating the emergence of parasites in winter and methods of preparing parasite larvae for examination and identification.

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